MOVEMENT PATTERNS, HOME RANGE AND DEN SITE SELECTION OF URBAN RED FOXES (*VULPES VULPES*) ON PRINCE EDWARD ISLAND, CANADA

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Faculty of Science

University of Prince Edward Island

Hailey J. Lambe

Charlottetown, Prince Edward Island

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Abstract

The opportunistic and adaptable nature of red foxes (*Vulpes vulpes*) in terms of habitat, diet and movement patterns, has contributed to their vast success in urban areas worldwide. Understanding the ecology and behaviour of urban wildlife, in particular carnivore species, is becoming increasingly important for reasons pertaining to management strategies, human-wildlife conflict prevention and wildlife health. On Prince Edward Island (hereafter PEI), foxes successfully colonized urban areas shortly after the establishment of eastern coyote (*Canis latrans*) populations in the 1980's, as an effort to avoid competition and conflict with the larger canid. The main objective of this thesis was to investigate key ecological indicators such as den site selection, home range size, habitat selection and movement patterns within Charlottetown in order to discern potential anthropogenic effects on the species.

Citizen science in combination with physical surveys was used over two years to locate and record measurements of fox den-sites within Charlottetown. In addition, logistic regression modelling was used to examine potentials relationships between environmental variables (land use type, distance to roads) and den site locations in order to identify factors associated with the occurrence of den sites within Charlottetown. Over 124 den site locations were recorded over the study period with mean distance to the nearest road found to be 95.9 ± SD 77.1 m. Den analysis results also indicated that the odds of finding a fox den within this urban landscape increased by 4-6 times in areas with minimal human disturbance.

Habitat selection and home range size were investigated through GPS-collared individuals (2 male, 4 females) over three seasons (summer, fall, winter). Results of minimum

convex polygon analysis indicated that the home range sizes of Charlottetown's foxes were similar to those found in rural areas and larger than those of foxes existing in other urban areas. Differences in the home range sizes of foxes in this study may be due to the availability and accessibility of resources within the urban matrix as well as seasonal challenges such as snow cover. Habitat selection results indicate that foxes in Charlottetown prefer to spend their time in land-use types that are less-disturbed by humans such as natural lands, agricultural areas and regions of low human use, further suggesting that these areas may provide a greater abundance of resources such as food, space and vegetative cover.

Movement data was also obtained from GPS-collared individuals and compared with theoretical predications in order to investigate the foraging behaviour of foxes in Charlottetown and how potential confinement effects, associated with the increased fragmentation of urban landscapes may affect movement patterns. Correlated random walk models were used as our null hypothesis for fox movement features of six foxes over three seasons (fall, winter, summer). Metrics examined included: net-squared displacements, turning angles, move length distributions and cluster detection. Our results indicated that despite the patchiness of urban environments such as Charlottetown, foxes are not demonstrating directional persistence that is associated with correlated random walks, but more random-like movement patterns. This could be due to an abundance of both natural and anthropogenic resources. The movement of foxes in this study also suggests that movement patterns may differ based on season as resource availability and accessibility may alter foraging patterns associated with snow cover and lower overall ecosystem productivity during the fall and winter.

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Chapter 1

General Introduction

1.1 Urban Wildlife

The earth's population has recently reached over 7 billion people (United Nations 2014). Not only are there a record number of humans on the planet today, but currently, the majority of these people are residing in urban rather than rural areas. Urban, as defined by Gehrt (2010), is an area of human residence, activity and associated land area developed for those purposes, which is usually defined by a threshold of population density. More than half of the world's population (3.9 billion) is presently living in urban areas around the globe, with predictions of that proportion shifting to two-thirds by 2050 (United Nations 2014). The continuous expansion of urban development is rapidly displacing wildlife populations worldwide resulting in more encounters between humans and wildlife every day.

Only in the past few decades have scientists regarded urban areas or cities as independent ecosystems (Sukopp 2002, Gehrt 2010). The wildlife inhabiting these urban ecosystems has consequently been classified differently than traditional wildlife. For instance, Adams et al. (2006) define "urban wildlife" as all non-domestic vertebrate species (e.g., mammals, fish, reptiles, amphibians, birds and plants) with populations existing in areas classified as urban. Wild animals may be drawn to urban centers as they may offer unexploited niches, non-seasonal food and water resources and reduced pressure from natural predators (Bateman and Fleming 2010). It is also possible that some species persist in areas that were originally wild, adapting to new environments as

urban development built up around them. By overcoming the new ecological barriers associated with urban development it is probable that wild species will successfully adapt to this new niche. The individuals that do adjust to novel selective pressures should therefore have greater success in urban environments as a whole (Lowry et al. 2013). This adaptation does not come easy, however, as many urban species are required to alter their ecology and behaviour in comparison to rural counterparts. Luniak (2004) describes some of the most characteristic adjustments of urban wildlife to be: 1) having to live at higher densities with smaller individual territories, 2) reduced migratory behaviour with alternative wintering possibilities in the city, 3) prolonged breeding season due to less migration and favorable microclimates, 4) longer lifespan due to increased food resources, 5) lower predator pressure and the reduction of migratory tendencies, 6) extended periods of circadian activity due to the artificial lighting found in cities as well as the preference to be more active at times when humans are not (e.g. at night). Some examples of wildlife that have successfully adapted to urban niches include: the rock dove (*Columba livia)*, raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), house sparrows (*Passer domesticus*), white-tailed deer (*Odocoileus virginianus*), and European Starlings (*Sturnus vulgaris*) (Ditchkoff et al. 2006).

Mammals and birds specifically can be classified into three distinct categories that reflect their ability to adapt to human presence (Goldstein et al. 1986, Maeda and Maruyama 1991, Blair 2001, Nilon and VanDruff 1987). Blair (2001) describes these categories as urban avoiders, urban adapters and urban exploiters. Urban avoiders are species that are sensitive to human presence and habitat disturbance and therefore tend to rely only on natural resources (Johnston 2001, McKinney 2002). Examples of these

"avoiders" include large mammals and predators that require lots of space and were actively persecuted by settlers and avian species that are naturally adapted to large, interior forests. Urban adapters are generally found in the suburban areas of cities, as they are able to utilize areas of human development, but also rely on natural resources (Johnston 2001, McKinney 2002). Common "urban adapters" include omnivorous avian species such as robins, crows, blue jays and seed eating finches that benefit from ornamental gardens and bird feeders. Some mammalian urban adapters, able to seek out shelter in areas of heavy human use, as well as exploit food sources provided by humans (e.g., garbage, backyard gardens, compost piles) include coyotes, foxes, skunks and raccoons (McKinney 2002). Finally, urban exploiters are species that are almost entirely dependent on human development. These species have been known to reach their highest densities in human populated areas due to a lack of natural predators and abundant food resources (Adams 2006). Urban "exploiters" include rock doves, starlings, Norway rats and the house mouse.

When reviewing the behavioural responses of urban adapter and urban exploiter species, Lowry et al. (2013) proposed that specific modifications of species behaviour may increase the chance of successful urban colonization. Such behavioural modifications include: bold temperaments which may allow the animal to take more risks in threatening situations, an extended annual reproductive period attainable by increases in year-round resources, adjusted foraging activity to coincide with low traffic/human activity and the ability to use human waste and infrastructure as viable sources of food and shelter. There exists a need for research into the behavioural patterns of urban wildlife in order to further enhance our understanding of the dynamic relationships

between wildlife and human environments. Through such research we may be able to predict which species are most likely to successfully live in harmony with humans, and which species may be at a higher risk of extirpation or extinction as a consequence of continuously expanding urban development (Sutherland 1998, Warren et al. 2006, Lowry et al. 2013).

1.2 Urban Carnivores

Medium-sized carnivores, such as the red fox and coyotes could be considered "ideal" urban dwellers as they exhibit a high level of plasticity in terms of diet, movement patterns and social behaviour (Bateman and Fleming 2010). The history of carnivores residing in urban areas likely stems from the close associations that humans have had with animals such as dogs and cats for thousands of years. Domestication is one way that has allowed for these animals to access regions of the world that would not normally be within their natural means. In addition to domestication, history dictates that wherever human settlements exist, wild carnivores have been observed close by whether it be by mistake, to scavenge on human refuse or to predate upon previously domesticated animals (Bateman and Fleming 2010).

Some urban carnivores such as coyotes, red foxes and raccoons are considered urban exploiters and are known for their innate ability for discovering the benefits of cohabitating with humans. It has been suggested that there are three key variables that influence the ability of a species to adopt a new environment: resources, natural enemies and the physical environment itself (Shea and Chesson 2002). In terms of resources, cities are extraordinary for offering stable, year-round food and water sources. Urban success for carnivores is partially attributed to the fact that most of these species are not

strictly meat-eaters, but omnivorous feeders. Rodents are an abundant source of food in most cities, as are birds and sometimes even domestic pets. Other sources of nourishment include insects, invertebrates, human refuse, pet food that is left outside, and food that is deliberately left outside to feed wild animals (Bateman and Fleming 2010). A study conducted in the city of Bristol (United Kingdom), found that 10% of houses were deliberately feeding foxes. Most of the households participating in fox feeding started leaving food out in order to get better and longer views of the animals or because the foxes appeared to be tame and thus they attempted to hand feed them (Baker and Harris 2004). Water availability is also high in most cities as the artificial watering of vegetation and gardens is common, as well as the occurrence of water retention ponds and flooding channels (Gehrt 2010).

Many carnivores take up residence within urban centers due to the lack of natural predators found here. Avoidance behaviour of foxes in the presence of coyotes for instance, may initiate the immigration of foxes into certain cities not occupied by coyotes (Voigt and Earle 1983). This is likely the case for urban areas such as Toronto, Canada, as evidence has been found to support such behavior and thus may explain the higher number of urban foxes in parts of Ontario that support both canid species. Immigration into urban areas may allow foxes to exist in an environment where competition for prey and territorial disputes with coyotes are slim to non-existent due to abundant resources. In addition, urban areas may offer species such as foxes, coyotes, raccoons and bobcats refuge from the major pressures of sport hunters and trappers that exist in rural environments. If then, these species are capable of maintaining resource levels and able

to successfully mate and reproduce, their chances of persisting in urban environments are high.

According to Shea and Chesson (2002), the last factor that may influence species selection of a new environment is physical characteristics of the environment itself. An urban habitat can potentially offer "green areas", such as golf courses, recreational playing fields, parks and large residential properties. These areas are crucial for daytime shelter, potential den site locations and may also contain a wide variety of natural food resources such as rodents and birds. In many cases human constructed corridors such as railway lines, power line passageways, beach strands or riverbanks, and flood or drainage lines link these green areas. These potential links offer a way to travel between habitat patches without using high human-traffic areas (Bateman and Fleming 2010). There are also specific types of human development that tend to be more attractive to wildlife species. For example, foxes of Bristol (United Kingdom) are known for their use of backyard gardens. The low-density intra-war housing style constructed in the early 1940's made relatively large gardens prominent fixtures of suburbia designs and thus backyards became fenced-in areas of semi-natural habitat. Red foxes flourish in this environment since the gardens provide a wide diversity of food sources, daytime cover and potential denning sites (Harris and Baker 2001, Soulsbury et al. 2010).

Denning carnivores such as bobcats, raccoons, foxes and coyotes are opportunistic animals and are known to exploit urban structures in order to construct a den. For instance, raccoons prefer hollow trees, even in an urban landscapes (Hadidian et al. 2010, Rabinowitz and Pelton 1986, Endres and Smith 1993) but will use a variety of alternate sites for denning, including rock ledges, brush piles, storm sewers, abandoned

burrows from other animals and accessible human structures such as chimneys (Stuewer 1943, Berner and Gysel 1967, Schinner and Cauley 1974, Rosatte et al. 1987, Hadidian et al. 1991, Hadidian et al. 2010). Many coyotes select den sites in areas of sandy loam soil for easy digging (Althoff 1980, Hallet et al. 1985, Harrison and Gilbert 1985, Grubbs 2009). Coyotes are also quite resourceful, and like raccoons, have been known to utilize human structures in creative ways. In urban landscapes, coyote dens have been reported in culverts under high-traffic roads, in the basements of abandoned houses, and even directly behind the screen for a drive-in movie (Froman 1961, Grubbs 2009).

Although urban living may be advantageous in many ways, there are also many disadvantages associated to living in such close contact with humans. For instance, an undisputable characteristic of urban ecosystems is the fragmentation of natural habitats and green areas (Gehrt 2010). Habitat fragmentation is the process through which continuous habitat is subdivided into smaller patches (Kelt 2000). These small patches of natural/green habitats, characteristic of urban areas, are likely to contain fewer resources for an urban carnivore than a large uninterrupted patch. Moving through the urban matrix to different habitat patches can be a risky endeavor for wildlife as these green spaces are usually separated by roads or highways (Gehrt 2010). Bateman and Fleming (2010) summarized the results from 29 studies indicating that road accidents are a major cause of mortality in urban carnivores. In that review, vehicular collisions are responsible for a high percentage of mortality of many urban species such as: badgers (57%), red foxes (40%), coyotes (31%) and bobcats (38%). Gerht (2010) found that vehicular traffic is the most challenging obstacle for carnivores to overcome in order to survive in urban areas. Furthermore, it is likely that juveniles, very young individuals and those involved in large

scale dispersal movements for the acquisition of new territories and mates are more prone to deaths caused by vehicle collisions (Baker et al. 2007).

A prominent disadvantage that stems from carnivores thriving in urban areas is the high risk of disease propagation. The increased levels of resources that carnivores are able to exploit in many urban areas may allow them to tolerate higher population densities in urban compared to rural settings (Bateman and Fleming 2010). These high densities, however, may facilitate the rapid spread of disease as contact between individuals is more frequent. Diseases such as sarcoptic mange in red foxes (Baker et al. 2000, Gosselink et al. 2007, Gehrt 2010), canine parvovirus in gray foxes (Riley et al. 2004, Gehrt 2010) and canine distemper in raccoons and striped skunks (Gehrt 2005, Gehrt 2010) are examples of diseases that have a higher prevalence in urban landscapes and thus such populations are at risk of sudden, rapid declines should there be a disease outbreak.

1.3 Urban Red Foxes

The red fox (*Vulpes vulpes*) is an example of an urban exploiter species. It has the largest geographic distribution of any wild carnivore in the world and is found in most of the Northern Hemisphere and many areas of Australia in habitats ranging from deserts to arctic tundra (Saunders et al. 1995, Soulsbury et al. 2010). Two of the main reasons the red fox is successful in such a broad diversity of habitat types are: 1) its body size - being a medium-sized carnivore small enough to remain somewhat inconspicuous, yet still possess the mobile ability to transverse long distances in search of resources and mates, and 2) its lack of specialization in dietary and habitat requirements (Harris and Baker

2001). The first records of red foxes infiltrating urban areas were in London in the 1930s (Teagle 1967, Soulsbury et al. 2010). Other urban populations were recorded in Melbourne, Australia in the 1940s (Marks and Bloomfield 1999), Zurich, Switzerland in the 1980s (Contesse et al. 2004) and Toronto, Canada in the 1990s (Adkins and Stott 1998).

The initial wave of movement into urban areas of Britain was thought to be facilitated by the construction of low density residential housing that included large backyard gardens that offered a wide variety of food and shelter options, encouraging the foxes to remain in the area (Harris and Baker 2001). Foxes, similar to other urban carnivores, may also colonize urban areas to reduce competition with other predators, to access abundant food sources which are easy to exploit or possibly to escape hunting and trapping pressures of rural habitats.

Physical characteristics of red foxes can vary slightly between continents; however for the most part remain quite similar. The weight of an average male fox is 6.5 kilograms whereas an average female is 5.5 kilograms (Lloyd 1980). The fur coloration of a red fox can exist in several variations with the most prominent being red, and less common being silver and cross colorations. In the "red" coloration the coat is reddish-orange with a white-grey underbelly. The fore and hind feet as well as the backs of the ears are black and the tip of the tail is white (Harris and Baker 2001). "Silver" foxes can range from completely black in color to a lighter grey with darker areas, both maintaining the white-tipped tail. The "cross" colour variation is only found in North America and generally the fox is a reddish color with the black stripe down its spine and across its

shoulders (Harris and Baker 2001). Foxes molt once a year in the spring and the coat is at its best, in terms of color, luster and density, during the winter months (Lloyd 1980).

Foxes generally live in small territorial groups consisting of a dominant breeding pair and non-dispersing offspring from previous litters which are typically female (Baker and Harris 2004). As in rural settings, these territorial groups have home ranges that rarely overlap. The density of urban foxes are typically 2-12 adults/ km^2 (Harris and Rayner 1986, Marks and Bloomfield 1999, Contesse et al. 2004, DeBlander et al. 2004, Rosatte et al. 2007, Soulsbury et al. 2010) but can fluctuate based on population density of an area. The city of Bristol in the United Kingdom reached the highest urban fox density ever recorded with 37 adults/km^2 before an outbreak of mange decimated the population in the 1990s. Not only did the mange epidemic drastically reduce the fox density of this area but it also permitted a shift in home range size. As foxes died of the disease, home ranges were left vacant and neighboring families took on the new home range in addition to their own. The average home range size before the mange outbreak was 26.9 ± 14.0 ha and increased to 209.6 ± 127.5 ha after the fox population declined by > 95% following the outbreak (Baker et al. 2004).

The reproduction process, as well as kit-rearing behaviours, appears to be similar amongst urban and rural red foxes. For instance, in both rural and urban environments dens can exist in the form of self-excavated burrows, a burrow previously used by another animal, spaces underneath garden sheds, or in abandoned buildings (Harris and Baker 2001). Females are monoestrus, being receptive to breed for 3-5 days a year (Tembrock 1957). In the Northern hemisphere, fox births typically occur between February and May after a gestation period of approximately 53 days. Normally only one

female per family group will produce offspring per year, but on occasion, especially in areas of high resource abundance, one den may be shared to raise separate litters (Harris and Baker 2001). Urban areas such as Bristol and London (United Kingdom) have records that indicate the average litter size of red foxes has been found to be 4.76 and 4.72 respectively (Harris and Smith 1987). Whereas rural litter size records have varied with an average of 3.3 in northeastern Spain (Martorell Juan and Gortazar Schmidt 1984), 5.0 in Prince Edward Island, Canada (Wapenaar et al. 2012) and 8.0 in Ontario, Canada (Voigt and Macdonald 1984). Such variation in litter size is likely due to factors such as habitat availability and climate patterns (Wapenaar et al. 2012) as well population densities and resource accessibility of the area (i.e., litter size increases if population density declines or resource abundance is high).

Young foxes are known to remain in the natal den for the first 3-4 weeks with their eyes opening after approximately two weeks. The kits start weaning at about three weeks of age (Henry 1986). At an age of three months the young are no longer being fed by adults and begin to independently hunt small prey items, such as invertebrates and earthworms (Soulsbury et al. 2008). Kits tend to remain in the area immediately surrounding the den for the first few months, but will increase the distance they travel away from the den every week. By five or six months old, young foxes are using almost all of their natal territory (Robertson et al. 2000). This is generally when juveniles begin to disperse in hopes of finding their own territory and mates. Sexual maturity is generally reached for both male and females at approximately nine months of age (Soulsbury et al. 2010).

Urban fox mortality can be inflicted by factors such as disease, lethal human control, infanticide and interspecific conflicts. The principal cause of death for foxes living within the urban matrix, however, is motor vehicle collisions. Activities such as foraging for food, finding a mate to breed with and territorial defense can influence the number of time foxes have to cross roads and highways (Baker et al 2007). Foxes are most vulnerable to vehicle collisions when juveniles are dispersing from their natal home ranges and during breeding season as males partake in a greater number of extraterritorial movement bouts (Robertson et al. 2000, Soulsbury et al. 2010). Several studies conducted in urban areas demonstrate variations in mortality rates with rates of 54%-57% being reported in Bristol (Harris and Smith 1987) while rates of 66%-68% have been documented in Illinois (Gosselink et al. 2007, Soulsbury et al. 2010). A study conducted in London, with a sample of 1628 dead foxes reports that 52% were less than a year old and only 3% survived to an age older than 5 years (Harris and Baker 2001). Although mortality rates may seem high in urban areas, in many cases urban foxes live to be older than rural populations due to the limitations on hunting and trapping within city-limits.

The red fox is an opportunistic omnivore that consumes a variety of food items, including fruits, berries, small mammals, insects and invertebrates, fish, amphibians, human waste and carrion (Soulsbury et al. 2010). Urban foxes will occasionally kill and eat domestic poultry and pets, although this is documented as a rare event. In Bristol only 0.7 % of households reported losing a pet cat to foxes in a 12 month study (Harris 1981). Anthropogenic food sources also play a fundamental role in the diet of urban foxes. Whether food is being left out purposely for wildlife or compost and garbage bins are simply left at accessible level, humans are contributing a lot of supplementary food for

urban fauna. A study done in Zurich, Switzerland reported 85% of households in the area provided anthropogenic food that was accessible to foxes. Seventy-five percent of this food consisted of human refuge and compost while the other 25% was made up of fruit, berries and food provisions for pets, birds and other wild animals (Contesse et al. 2004). Another study conducted in Bristol (United Kingdom) indicated that before the outbreak of mange, as much as 10% of households were purposely supplying food for the foxes (Baker et al. 2000, Soulsbury et al. 2010). This high level of feeding can promote a "tameness" in urban wildlife such as foxes. This is unique to species living in such close association with humans where they no longer fear humans but regard them as an opportunity in which to obtain food (Adams et al. 2005, Luniak 2004).

1.4 History of Red Foxes on Prince Edward Island

The red fox (fox) is indigenous to Prince Edward Island (PEI) and observation records of the species date back to 1765 when Samuel Holland surveyed the Island for the British government (Holland 1965, Curley 1983). The fox remained the largest native mammalian predator on PEI until the arrival of the eastern coyote (*Canis latran*s) in the 1980's (Personal communication, PEI Department of Fish and Wildlife 2013). Being a small Island (5,657 km^2 (Whiteside1965)), lacking inaccessible wilderness areas, PEI's fox population has always been highly accessible to man. Animals such as beavers, fox, mink, otter and seals have been actively hunted in North America for their furs since the 1600's. This fur-trading boom was initiated by the fashion industry as fur coats gained popularity. Near the end of the nineteenth century it became apparent that the fur-trading market could not possibly keep up with the demands of the fashion world (Stresman 2006).

During this fur boom, it was the silver coloration of the red fox that sold for the highest price at fur auctions, and these coats were particularly popular among the nobles of the Russian Empire (Bourrie 2012). It was this wealthy customer base that encouraged two native Islanders to experiment with capturing, domesticating and breeding silver foxes for their fur. By 1900 Charles Dalton and Robert Oulton had discovered a successful methodology for breeding silver foxes and received $1,807.00 that year for a single pelt (Bourrie 2012). This was only the beginning of the fox farming industry in PEI, with the major boom taking place between 1910 and 1914. During this time there were more than 60 operational ranches housing over 3000 foxes (Stresman 2006).

Fox farmers continued to make a fortune into 1920's but the market began to fall as the Depression ensued and World War II broke out in Europe in the 1930's. At this point the silver fox market was saturated, as fox farms existed all over the Northern hemisphere and therefore the value of the furs declined sharply. Although there was a slight recovery in the market from 1942-1945, afterwards it continued its drastic descent (Clark 1959, Curley 1983). Although many locals living in close proximity to fox farmers suspect that farmers released captive foxes into the wild following the fur market's decline, no evidence of such actions was ever discovered (Curley 1983).

During the 1950's and 1960's the foxes on PEI were declared an agricultural nuisance and a bounty of $2.00 was offered per pelt. Throughout this period approximately 1900 fox pelts were returned per year. This bounty was withdrawn in 1964 (Heyland 1965, Curley 1983). Today, an annual fur-trapping season exists in rural regions of PEI from November 1st to January 31st for licensed trappers. At the 2014 North American Fur Auctions, red fox pelts were worth an average of $56.41 with a top price of

$320.00, while the silver fox pelts went for an average of $52.11 with a top price of just $80.00 (North American Fur Auctions, 2014).

In the 1980's the fox populations of PEI experienced a shift in distribution as eastern coyotes emigrated from mainland New Brunswick via the ice covered Northumberland Strait. Although no studies have yet been conducted with respect to the interactions between these two canids in PEI, it is speculated by wildlife officials that the establishment of coyote populations across PEI, affected fox populations in a variety of ways. For instance, it has been observed that shortly after the arrival of the coyotes, red foxes began to move into urban areas (personal communication, B. Potter and C. Gallison, PEI Department of Forests, Fish and Wildlife). This type of avoidance behaviour has been documented in other regions of Canada where ranges of the two species overlap (see Voigt and Earle 1983). Because the two carnivores compete for the same food and space resources, the foxes tend to be displaced by the bigger canid in order to avoid conflict (Voigt and Earle 1983, Sargeant and Allen 1989). This is likely the reason for foxes moving into the urban areas of PEI. Although actual abundance levels of urban foxes are not known, the comments and complaints from the public suggest that, not only have numbers increased since the initial shift into PEI's urban areas, but that the foxes are adapting extremely well to city life (personal communication, B. Potter and C. Gallison, PEI Department of Forests, Fish and Wildlife)

Human perceptions of, and attitudes toward, wildlife can be complex and dynamic especially when dealing with predators (Butler et al. 2003, Soulsbury et al. 2010). Experiences with urban carnivores can be negative (e.g., spread of disease, motor vehicle collisions, threats to domestic pets, disruption of gardens, etc) or positive (e.g.,

observing animals in an area where wildlife is scarce). Most complaints regarding urban foxes stem from house owners who grow frustrated with the noises associated with mating, damage to property inflicted by a litter of growing cubs or because of food and other debris that accumulates at den sites in the spring (Harris and Baker 2001).

On PEI, the relationship between humans and urban foxes is unique in that the majority of residents consider foxes charismatic animals that they are proud to have around. In fact, a recent survey conducted on PEI (n= 150) indicated that > 50 % of people residing within Charlottetown and > 30 % of people living outside of Charlottetown (n = 39) demonstrate positive attitudes towards the presence of foxes on PEI (Martin 2015). In a similar survey, 32% of people in the Charlottetown area (n = 256) have admitted to feeding the foxes in the past, or being willing to feed them in the future (Martin 2015). In many cases foxes are being fed on a daily basis to encourage them to return to their property (Personal communication with Charlottetown residents, 2014). In extreme cases the animals are thought of as pets and are even given names. This unique relationship likely exists due to the low risk of serious zoonotic disease transmission. In many parts of the world red foxes are a major vector for severe diseases such as rabies, echinococcosis and sarcoptic mange that can be contracted by both domestic pets and humans (Soulsbury et al. 2010). So far, these diseases are not established on PEI and so humans tend to not associate foxes with major health hazards. There exists, however, a need to educate the public about other parasites and diseases that PEI's urban foxes can potentially harbor and spread such as *Toxocara canis*, which can be transmitted by coming into direct or indirect contact with fox feces (Personal Communication, Dr. Gary Conboy, Atlantic Veterinary College 2014). In order to

achieve a healthy and harmonious relationship between urban red foxes and humans, it is imperative that we continue to learn as much as possible about their evolving behaviour and ecology. It is also important to convey this information to the general public in a way that emphasizes what is best for both, the animal and human safety.

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Chapter 2

Den site selection of urban red foxes (*Vulpes vulpes*) on Prince Edward Island, Canada

2.1 Abstract

Red foxes are currently the most successful carnivore to colonize urban areas worldwide due to their opportunistic nature and adaptability. Foxes began to colonize the city of Charlottetown, in the province of Prince Edward Island (PEI), Canada after the establishment of coyote populations in the 1980's and have continued to be successful in urban areas across the province. There exists a need to better understand den site selection in urban foxes in order to promote harmonious relationships between wildlife and city residents as well as for the implementation of successful management strategies, should they become necessary. In this study, citizen science and physical surveys were used to locate and record measurements of fox dens in Charlottetown. Logistic regressions were implemented as a species-distribution modelling technique to examine the relationships between environmental variables (i.e.; land use type, distance to roads) and den site locations to identify factors associated with den sites within this urban environment. Of 124 dens found over two years, 92 were found in natural areas or areas of low human use and 32 dens were found on residential properties. Significant differences existed in entrance height, entrance width and entrance elevation between dens found in residential vs. non-residential properties (two tailed t-test, $p < 0.001$). Mean

distance to roads from observed dens was 95.9 ± SD 77.1 m. Results from logistic regression models suggest a consistent increasing trend of finding a den the further travelled away from roads ($p = 0.061$), up to a maximum of 100 m. Additionally, the odds of finding a den is 4-6 times greater in areas of Charlottetown that contain natural areas or areas of low human use compared to those areas with neither. Our results indicate that a key component in the den site selection of urban foxes on PEI is the lack of regular disturbance by humans. Although they are able to adapt to high human (residential) areas for denning, they prefer more natural habitats, and likely utilize areas of high human use (i.e.; roads, backyards) to easily access profitable resources.

2.2 Introduction

In recent years, the expansion of urban areas around the globe, has resulted in the colonization of cities by many different avian and mammalian species (Luniak 2004). The red fox (*Vulpes vulpes)* (herein fox) has proven to be one of the most successful species to colonize urban areas with widespread populations confirmed in cities like London, England (Harris 1977, Page 1981), Toronto, Canada (Adkins and Stott 1998), Melbourne, Australia (Marks and Bloomfield 1999), Berlin, Germany (Schoffel et al. 1991) and Copenhagen, Denmark (Willingham et al. 1996).

Embedded natural areas become generally reduced as urban areas are developed, a fact that can be problematic for denning species such as foxes and coyotes. Although both species require secure daytime rest sites and suitable substrate for digging dens, foxes are more likely to be present in areas of high-human density (Harris 1981). For example, many urban areas in Britain boast a housing style that provides large backyard

gardens. Despite being in close contact with city residents, these spaces offer vegetative cover and lower degrees of disturbance providing foxes with optimal daytime resting sites (Harris and Rayner 1986, Bateman and Fleming 2010). Foxes have also been known to dig dens underneath anthropogenic structures such as garden sheds and unoccupied buildings (Harris and Baker 2001). In contrast, coyotes are less willing to occupy land in close proximity to humans and are generally found residing in patches of natural forest, scrubland and vacant lots within cities (Atwood et al. 2004, Atwood 2006, Baker, 2007, Bateman and Fleming 2010). A survey done in Cape Cod, US, for instance, discovered all coyote dens were located in natural wooded habitats at least 300 m away from the nearest human residence (Way et al. 2001).

Although selecting adequate den sites in urban areas may be challenging for canid species, areas such as natural forest stands, flood channels, the edge of power line corridors, and areas of exposed coastline may provide sufficient cover and connectivity between habitat patches to sustain healthy populations (Lewis et al. 1993, Bateman and Fleming 2010).

There currently exists a lack of information regarding the denning behaviours of foxes in urban areas. The majority of studies conducted on this topic examine den site characteristics in rural or natural habitats. It is, however, known that foxes are opportunistic animals not only in terms of the food that they consume, but also in terms of den-site selection and therefore preferences may change based on geographic location (Soulsbury et al. 2010).

To date, there have been no studies done on red fox den-site selection in neither urban nor rural environments in the province of Prince Edward Island (PEI), Canada.

Foxes began to colonize urban areas of PEI in response to the immigration of the Eastern coyote (*Canis Latrans*) to the Island in the 1980s presumably to avoid competition with the larger canid. Since then, foxes have shown extraordinary adaptation to PEI's urban environments. Evidence suggests that urban fox populations on PEI have increased over the last decade (personal communication, Brad Potter and Chuck Gallison, PEI Department of Forests, Fisheries and Wildlife). As numbers increase, so does the possibility of conflict between humans and foxes. Hence, there exists a greater need to know more about the species for future management programs.

Fox dens are important as they provide the shelter necessary for the birthing and rearing of kits each spring. Fox dens can take on many different appearances, but are generally composed of a burrow system dug directly into the ground, and commonly into the side of a slope (Henry 1986). Although some dens may have a single entrance, they are typically constructed with multiple entrances to facilitate quick escape routes if necessary. The kits are often found in either, an enlarged chamber of the den, or at the blind end of the burrow system (Lloyd 1980). These underground dwellings provide shelter and warmth for new born kits who will remain in this refuge for up to 6 weeks (Lloyd 1980). In many cases it is normal for vixens to not only excavate a den for the purpose of birthing and kit-rearing (natal den), but also to excavate smaller temporary den sites within her territory for extra protection. In addition, if the female feels threatened or experiences human-related disturbances it is normal for her to move her family to the alternate den site as a temporary retreat (Henry 1986).

The number of entrances a fox den has is highly variable. Sheldon (1950), for instance, inspected 50 den sites in New York State and found that the number of

entrances ranged from 1 to more than 20, and similarly another study done in Alaska, found between 6 and 19 den entrances (Murie 1944). The number of entrances a den has may be determined by how many foxes utilize the den, and how often it is used (Arjo et al. 2003). For example, a natal den site, where kits spend the most time during kit-rearing may possess a greater number of entrances than a temporary retreat. If there is a large litter, or more than one family uses a den site it is also more likely that additional entrances will be created. In many cases, large natal dens are used for multiple kit-rearing seasons and each year new entrances may be added to adjust for varying litter sizes (Nakazono and Ono 1987).

Den sites are important elements in the successful growth and development of young foxes. Active selection of these den sites is therefore based on key environmental, ecological and physiological requirements (Uraguchi & Takahashi 1998). This selection is imperative as dens provide a refuge, microclimatic stability and shelter for foxes throughout the year (Artois 1989; Reichman and Smith, 1990; Laureson, 1994; Ruiz-Olmo et al. 2003). Foxes utilize their dens most prominently during breeding and kit-rearing seasons which occurs in the spring. Den sites may also be visited less frequently throughout the year for the purposes of transient resting shelters and for territorial scent marking (Nakazono and Ono 1987).

In many parts of the world, foxes in rural environments will use burrows already excavated by other mammals such as badgers or rabbits as their den sites, often enlarging them for more suitable accommodation (Marks and Bloomfield 2006). The selection of previously excavated burrows varies, based upon fossorial (burrowing) mammals within the region, soil composition and habitat requirements of the fox. In areas of Germany, for

example, most fox dens were found to be old badger setts (Stubbe 1980) whereas in western China, natal fox dens were predominantly located within burrows originally dug by the Himalayan marmot (*Marmota himalayana*) (Wenyan et al. 1995, Marks and Bloomfield 2006). In regions where soil structure is somewhat porous and easy-to-dig into, however, it is common for foxes to excavate their own dens (Weber 1982). In urban areas, due to the lack of fossorial mammals, foxes are known to dig their own dens, in many cases digging underneath manmade structures such as: patios, garage floors, and even grave stones (Marks and Bloomfield 2006, Harris and Baker 2001).

Kosolov (1935) suggests that the internal structure of a fox den depends on the condition of the soil in which the den is constructed. In areas of clay soil, dens consisted of shallow burrows with many branches whereas in regions of sandy soil, dens were much deeper with fewer branches. Many studies suggest that, for both urban and rural den sites, foxes prefer to dig dens in areas of sandy loam (e.g., Soper 1942, Murie 1944, Sheldon 1950, Ruiz-Olmo et. al., 2003). This type of substrate is clean and permeable which enhances the water-draining capabilities of the den site. In many cases foxes also prefer den sites to be located on a slope or hill (Henry 1986, Goszczynski 1999, Goldyn et al. 2003). Possible explanations for this include: effective drainage, easy soil excavation (Uraguchi and Takahashi 1998) and a better chance of hiding den entrances (Goldyn et al. 2003). Den sites may also be selected based upon the amount of sunlight exposure available to kits in nearby areas as shown in a study conducted by Uraguchi and Takahashi (1998). Nakazono and Ono (1987) suggest that juvenile foxes require substantial amounts of sunshine for normal growth and therefore it may be desirable for den site locations to be located near the edge of woodlands, or near a clearing so that both

shelter and sun are provided. Another selection criterion may be the orientation of the den site itself. This preference for directional orientation of the excavation is related to optimal microclimatic conditions (Krim et al. 1990). The arctic fox, for example has demonstrated preference for southern facing entrances, which are thought to take advantage of warmer exposures during kit rearing (Chesmore 1969, Smits et al. 1988). It is conceivable that red foxes in northern latitudes may demonstrate this type of selection as well.

The most essential factor in determining den site selection in urban areas is the lack of regular disturbance by humans (Storm et al. 1976, Harris 1977, 1981, Uraguchi and Takahashi 1998). This was demonstrated in large cities such as London (Harris 1977), Toronto (Adkins and Stott 1998) and areas of Western Switzerland (Weber and Meia 1996). Marks and Bloomfield (2006) conducted a study in Melbourne, Australia where they located 72 fox dens in urban areas of the city. Many of the dens examined in this study were located in areas where human disturbance was low or restricted to daytime use only. Despite establishing den sites underneath anthropogenic structures in Melbourne, 75% of these dens were located under buildings that were either unoccupied or occupied by a single resident. Thirty-nine percent of dens were found in other areas of low human disturbance including: cemeteries, areas along creeks, railway easements, urban water reservoirs and golf courses.

In the United States and Canada, foxes are inclined to utilize small road culverts for shelter in urban areas (Gosselink et al. 2007) as well as open green spaces located within the urban matrix (Adkins and Stott 1998). A study done by Adkins and Scott (1998) in the Greater Toronto Area located 20 den-sites, most of which were found to be

on golf courses, in parks containing lots of bushes and shrubs or in a system of ravines found in an area surrounded by residential development.

As previously mentioned, in many urban areas, red foxes are known to utilize the space beneath current human infrastructure as den sites. In Melbourne (Australia), for example, buildings constructed of weatherboard are the preferred building type selected by foxes for natal dens. These buildings tend to be elevated from the ground leaving approximately a 1-meter space between the floorboards and the ground which is ideal for a den site (Marks and Bloomfield 2006). In the city of Bristol (United Kingdom), inter-war style housing development provides ideal habitats for urban foxes as well. The large and established gardens and hedgerows that accompany this type of housing development, as well as the older population demographic that tend to occupy these areas allow for plenty of daytime shelter and limited disturbances (Harris 1981, Bateman and Fleming 2010). Approximately 40% of dens in Bristol are dug beneath utility sheds in these large gardens (Harris 1977, Page 1981).

It is known that the spatial distribution of various wild species is greatly influenced by access to suitable shelter sites such as dens (Elton 2001, Lindemayer and Fischer 2006, Morrison et al. 2006, Carter et al. 2012). Thus In order to maintain a harmonious relationship between foxes and humans in urban areas, it is imperative to understand the factors that drive den site selection. With this knowledge, those who are not fond of having these carnivores in close proximity to their homes may be able to alter their properties in a way that will deter the animal from selecting a den site there. From a wildlife management perspective, being able to predict the occurrence of den sites based on environmental variables may also be important in the case of zoonotic disease

outbreak and the resulting control tactics as well as limiting the impact of foxes on prey species (Carter et al. 2012).

The main objective of this study was to survey and map the location of fox dens in Charlottetown and describe the physical characteristics of each den (i.e., number of entrances, dimensions of entrances, etc.) An additional objective of this study was to determine if there was a relationship between den site selection and land use type. In particular we wanted to assess whether foxes were selecting den locations based on the presence of humans. We expected that the physical measurements of urban dens on PEI would be comparable to rural dens and that the distance to major human infrastructure such as roads and buildings would act as an important predictor for den site selection, such that dens were located farther away.

2.3 Materials and Methods

2.3.1 Study area

Charlottetown is the capital city of the province of PEI, as well as the largest urban area in the province. For this study, the adjacent town of Stratford (population of ~8,500, in 2014) was also included in the study as it lies in very close proximity to the capital city. Therefore, Stratford will hence forth be included when discussing "Charlottetown" (see Figure 2.3.1). The population of Charlottetown is approximately 43,000 which makes up the majority of the Island's urban population of 67,252 (PEI Statistic Bureau, 2014). Charlottetown encompasses an area of 67.4 km^2 (PEI Department of Environment, Energy & Forestry, 2010) along the southern shore of the province and is constrained by the Hillsborough River and the North River with much of the city being

exposed to the Charlottetown Harbor. Urban development is prominent along the waterfront with suburban areas stretching to the east, north and west with pockets of commercial development towards the northern perimeter (see Figure 2.3.1). Along with urban and suburban development, Charlottetown boasts over 158 parks and green spaces that make up an area over 2.2 km^2 throughout the city (City of Charlottetown, 2010). Another prominent landscape feature in the city is the 0.64 km^2 of agricultural land belonging to an Agriculture Canada crops and livestock research station (Agriculture Canada, 2014). Den data were collected in most areas of Charlottetown, however, the few regions that were excluded from analysis were areas where access was limited or restricted (see Figure 2.3.2).

2.3.2 Den Sites

Conducting den surveys in urban areas is challenging due to the large amount of private property located in cities. Attempting to gain individual landowner permission to survey small plots of land can be time consuming and inefficient. Citizen science is a data collection tool that is gaining popularity in many urban ecosystems. Formally defined, citizen science is a method by which the researcher determines the research questions and designs the experiment, while volunteers help to collect data which is to be analyzed and interpreted by the researcher (Lepczyk et al. 2004, Colding et al. 2006, Cohn 2008, Weckel et al. 2010). By asking public organizations and urban residents to report and submit relevant data to specific research platforms, researchers are able to quickly expand their access to private lands while also gaining active public interest in particular aspects of wildlife research (Cooper et al. 2007). Integration of scientific data collection, via the public, has become an established methodology in urban ecology, successfully achieving

results in areas of wildlife population trends (Hochachka et al. 1999, Cannon et al. 2005, Cooper et al. 2007), avian life histories (Cooper et al. 2005) and management regimens (Rosenberg et al. 1999, Gregory et al. 2005). This technique has shown to be especially useful in determining den site locations of urban foxes (Marks and Bloomfield 1999, Marks and Bloomfield 2006) and coyotes (Dodge and Kashian 2013) worldwide.

In the months of March – June (2013 and 2014), citizen science was employed to gain information about the location of dens in urban areas of PEI. This was done by asking residents through radio interviews, newspaper articles and social media to report den locations to our website (www.upei.ca/redfox) or to our Facebook page (https://www.facebook.com/UPEIUrbanFoxProject). The locations of reported dens were then confirmed with site visits by identifying characteristic signs of den use including: evidence of prey animal remains such as bones and feathers, fresh scat, the accumulation of freshly dug dirt or entrances with hard packed soil, chewed objects, fox hair caught around entrances and visual observations of foxes in the area (Kolb 1985, Marks and Bloomfield 2006).

In addition to using direct observations of den sites via the public, a map was created based on fox sightings, using QGIS and Google Maps, to identify areas heavily used by foxes, including public green spaces and privately owned land.

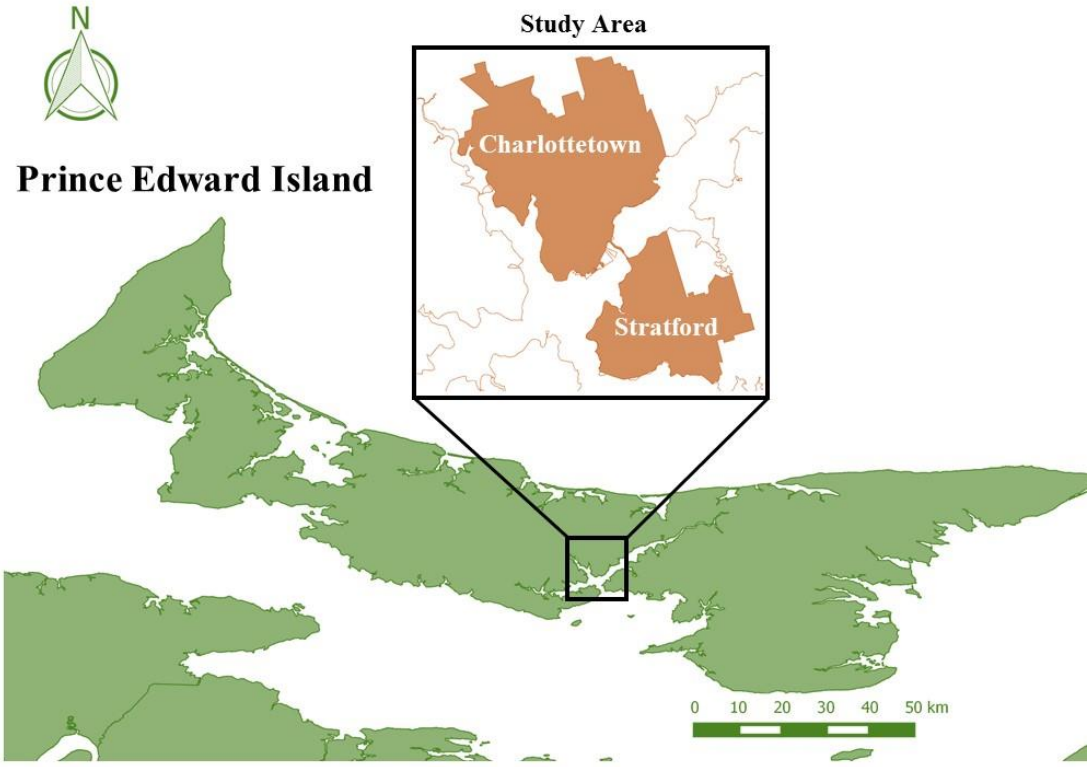

Figure 2.1. Map showing the boundaries of the study area including the capital city of Charlottetown and the adjacent town of Stratford, Prince Edward Island, Canada.

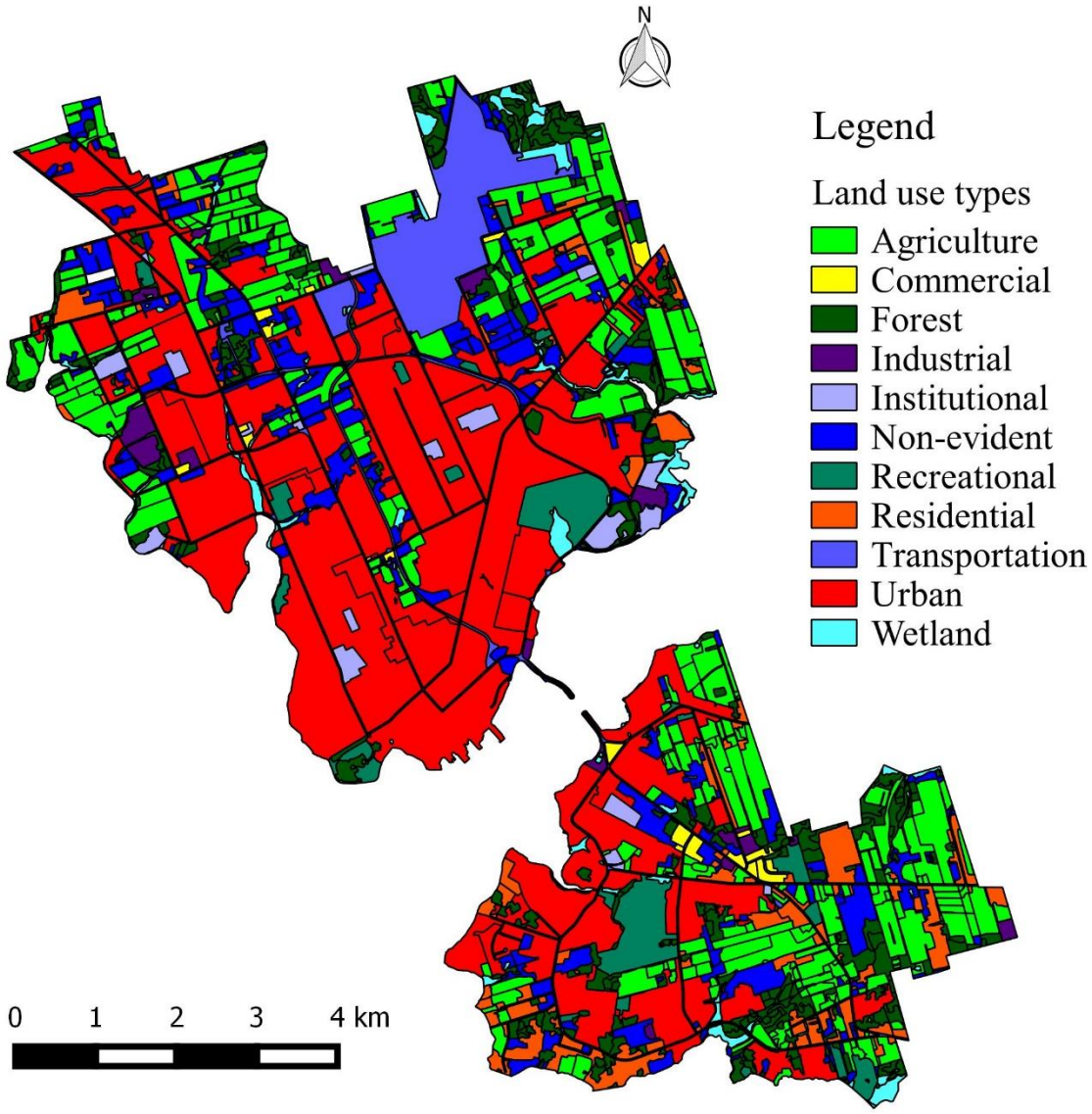

Figure 2.2. Map showing original land use classification (2010) of the study area, Charlottetown, as well as areas that were excluded from our study. These areas were excluded due to lack of access and lack of observation of foxes here.

Physical surveys were then conducted in these areas at least twice per week (pending landowner's permission) to look for signs of trails in the grass characteristic of repetitive fox movement, excavated dirt, and young foxes. Google maps were utilized for this process as this open-source service hosts an extensive collection of geo-referenced satellite imagery with resolution of up to approximately 0.5 m (Google 2013). Horizontal and vertical positional accuracy for google maps has been found to be 1.59 m and 1.7 1m respectively (Becek et al. 2011). The geographic location (longitude and latitude) of each den site was determined using handheld GPS units (~ 3 m Garmin eTrack, USA).

Confirmed den sites were revisited in July and August of 2013 and 2014 when intense kit rearing had ended, as to not disturb the families, to record physical characteristics of each den site. These characteristics included: the number of entrances, the height and width of each entrance and the approximate vertical height from flat ground to the center of the primary entrance (measured to the closest cm with a metric tape measure) and the cardinal direction that the primary entrance faced (measured with a magnetic compass). The vegetation that existed within a 10 m radius from the den site was also categorized into; manicured lawn, short grass (< 20 cm in height), long grass (≥ 20 cm in height), shrubs/bushes or trees. Two-tailed t-tests were used to identify if differences existed in the physical characteristics of dens sampled in 2013 and 2014 to determine whether these characteristics changed from year to year, dens that were occupied versus unoccupied when surveyed and also between dens associated directly with human infrastructure versus those that were not.

2.3.3 Distribution Mapping Models

Understanding the variables that influence the spatial distribution of a species can help identify key ecological processes responsible for ecosystem health and biodiversity (Brown et al. 1995, Carter 2012). Species distribution models (SDMs), can be defined as associative models relating presence data (i.e. known locations of individual species) to information on environmental characteristics of those known locations (Elith and Leathwick 2009, Cassini 2011). Similar to the methods used by (Carter et al. 2012), the concept of SDMs were adapted to our data using the information associated with known den site locations or presence in place of the information associated with known locations of individual animals. In recent years, species distribution modelling has continued to gain popularity in the ecological world due to the vast improvements in data collection techniques such as global positioning systems (GPS) and geographical information systems (GIS).

Many researchers are using SDMs to gather information from point observations of a species and the environmental conditions that exist there, to predict the occurrence of species in regions where survey data are lacking (Franklin 2009). When statistical models, such as these, demonstrate a good fit between the species distribution and the environmental predictors that are being investigated, they can provide information into specific habitat preferences of that species, which can then allow for a spatial prediction of species distribution, or in our case den site locations, based on environmental characteristics. These predictions could be imperative for conservation efforts, environmental assessments and the implementation of management plans.

Many studies have gained insight into den site selection by conducting physical surveys locating dens sites and measuring physical characteristics of the den itself as well as surrounding areas (Nakazono and Ono 1987, Weber 1982, Meia and Weber 1992). The problem with any survey, however, especially in urban environments is that they are not exhaustive. The possibility of predicting the potential location of dens that were missed during the surveys (data collection) is important, and very useful from a wildlife management standpoint.

One common methodology used in ecological studies to predict the presence of a species in relation to environmental predictors involves comparing the distribution of presence records to that of pseudo-absences (Pearce and Boyce 2006, Franklin 2009). Pseudo-absences, in this case, are randomly generated locations within the study area that are used to characterize the full scope of the available environment (Franklin 2009). This type of presence - pseudo-absence model is particularly useful when dealing with binary response variables and also when trying to predict presence in areas inaccessible for surveying (i.e., as in this study, it may be urban areas with excess amounts of private property). With this approach we are able to extrapolate the distribution of dens beyond what is known by relating presence of a den to corresponding environmental factors. We can then contrast the distribution of present dens to that of pseudo-absent dens to predict the relative likelihood of a den being in an area given the environmental characteristics of that area.

In order to analyze presence – pseudo-absence data, generalized linear models (GLMs) are one of the most common statistical approaches used in ecological studies and have been known to perform better than alternative methods such as tree based methods

and genetic algorithms (Ferrier and Watson 1996, Pearce and Boyce 2006). Logistic regressions are a type of GLM that are used to model binary outcomes, as they are best able to cope with the binomial distribution.

There exists little guidance in the literature on how to randomly choose the locations of pseudo-absences. While Carter et al (2012) used a 1:1 ratio of den to non-den locations, we chose to follow a 2:1 ratio of randomly generated pseudo-absent dens to actual dens to increase the study sample size, as is commonly done in case-control studies (Dohoo 2009). When presence records are low or rare, many statisticians recommend that the sample size necessary for a logistic regression be at least ten times the number of explanatory variables (Peduzzi et al 1996, Lobo and Tognelli 2011). In the case of our study, however, presence records (n=98) are relatively high in relation to the area being sampled (67.4 km) and so selecting a large number of pseudo-absences is not as important. One advantage of choosing a low ratio of pseudo-absent den site locations to presence locations within our study was that it prevents the probability outcomes from being unavoidably biased towards the highest number of pseudo-absences used (Hosmer and Lemeshow 2000). Following the recommendations of Lobo and Tognelli (2011) for using a small number pseudo-absences, pseudo-absence locations were randomly selected in areas falling outside of the environmental envelopes defined by observed den site locations. In our case this envelope was the 50 m buffer zone surrounding each den which was determined to be the area most intensely used by the fox family during kit-rearing.

When using pseudo-absence data points, it is important to remember that the results from logistic regression models do not necessarily represent the probabilities of presence, but instead aim to predict the relative likelihood of presence (Pearce and Boyce

2006). Although this type of model can be used to investigate data collected over many decades through historical records, general performance tends to be better when using high quality survey data, generated by recent advances in GPS technologies (Pearce and Boyce 2006). Incorporating high quality survey data into logistic regression models have demonstrated superiority over alternative approaches and have proven to be quite powerful in predictive nature (Franklin 2009).

2.3.4 Identifying environmental predictors for den sites

Environmental data on land use, public roads, buildings, and bodies of fresh or brackish water were obtained from the Government of PEI GIS Data Catalog (error of approximately 5 m, L.R.I.S., 2005(a), L.R.I.S., 2005 (b) and the PEI Department of Environment, Energy & Forestry, 2010). These datasets were used to generate predictors of interest, namely (1) the distance from dens to features such as buildings, roads and water sources and (2) the presence of different land use categories in areas surrounding the den sites within 50, 100, and 150 m buffer zones. For the purpose of this study, Charlottetown's multiple land use categories were consolidated into four simplified classifications (Table 2.1). The initial buffer zone, a circle with a radius of 50 m, was based on observational evidence that the majority of intense kit-rearing occurs within this area (personal observation by Hailey Lambe, 2013). Therefore, we decided to use landscape features included in this area to help us determine important aspects of the den site selection process. Unger (1999), who was studying the denning habits of timber wolves in Wisconsin also used an area of 50 m radius from the den site as this was deemed an area of heavy use where signs significantly increased. Additional buffer zone sizes (circles with radii of 100 m and 150 m) were also evaluated. The largest buffer zone

size of 150 m (~ 7 ha) was chosen based on similar areas of red fox core use previously found in PEI (Silva et al. 2009). Although the data from Silva et al. (2009), were collected in more rural areas, we chose the smallest of the core use sizes found in this study to investigate, as home ranges and core use areas are known to decrease in size in urban areas (Bateman and Fleming 2010). We also chose to investigate the buffer size of 100 m as an intermediate area between observed high-intensity use and recorded core-use sizes. Land use types (agriculture, natural areas, areas of low human density and areas of high human density) were quantified for each of the various buffer zones (QGIS version 2.4, 2014; zonal statistics procedure). Fisher's exact test (Fisher 1922) was used to determine significant differences between the quantity of land use types present in actual den site buffer zone versus those present in pseudo-absent den buffer zones.

All spatial data were manipulated and analyzed using Geographical Information System (GIS) software QGIS. The distances from den sites (both real and pseudo-absent) to their nearest road, building, brackish water source and non-brackish water source were calculated using the GRASS plugin within QGIS (version 2.4, 2014; v.distance procedure).

A logistic regression, with the presence of den as the outcome (1 = observed den, 0 = pseudo-absent den), was used to identify environmental predictors for the occurrence of den sites. Initially, each land use variable was included as an unconditional predictor in the logistic regression and assessed over the different buffer sizes with Akaike Information Criterion (AIC) model selection techniques (Burnham & Anderson, 2002) to determine which buffer sizes provided the best fit to the observed data. Pearson's correlation matrices were constructed to determine if correlations existed between the

environmental variables we were interested in (i.e., distance to roads, buildings and water sources) and land use types. The value of "strong" correlation, however, is somewhat subjective in the literature as in many cases it is dependent on what is being measured. For the purposes of this study we excluded variables which produced correlation coefficients > 0.4. According to many statisticians this value is considered moderate to strongly correlated (Dancey and Reidy 2004, Lund and Lund 2015, Soleimannejed 2004). The model building process also included an assessment of linearity between the predictors and the outcomes; non-linear relationships were modeled using linear splines (refer to Franklin 2009 Figure 6.1). A stepwise approach was taken to build the logistic regression models, as this process allows for both forward and backward approaches and is overall more inclusive. From this model, an odds ratio for each predictor variable was determined. An odds ratio is the main measure of association between the predictor variables and the outcomes in logistic regression modelling, and is the only measure of strength applicable to case-control studies (Dohoo 2009). More specifically, the odds ratio represents the constant effect of a predictor (x), on the likelihood that one outcome will occur. For our model, the predictors are distance to roads ($\leq$ 100 m and > 100 m), and different land use types (natural areas and low human-use areas) while the outcome is the probability of finding a den. With respect to the land use types used in this model, the baseline, referring to the variable group against which all other variables were measured, was considered to be areas that contain no human use and no natural areas. Models were then evaluated with the Hosmer-Lemeshow goodness-of-fit test (Dohoo 2009). All statistical analyses were conducted using Stata 12 (Stata Statistical Software 2011), and statistical significance was set at $p < 0.05$.

Lastly, in QGIS, we generated points at 5 m intervals throughout the entire study area of Charlottetown and measurements were taken from each point to the nearest road. This was done to determine the possible range of distances from roads that are available to foxes in this study site, to serve as a benchmark for comparison. This information allowed us to determine if the results produced by the logistic regression model, regarding den site preferences in relation to distances to nearest roads, were representative of foxes actively selecting areas for den sites, or if they are if they were simply a consequence of Charlottetown's urban structure.

Table 2.1. Modified land use classification scheme of Charlottetown where high-density human use areas are defined as those areas used by humans every day, all year round. Low-density human use areas are defined as areas used less by humans for specific purposes in specific seasons (i.e. golf course) or areas that are rarely visited by humans.

Modified land use classification	Land use categories included
Agriculture	Agriculture (Experimental Farm)
High human use	Urban, residential, transportation, commercial, industrial, institutional
Low human use	Recreational, non-evident (abandoned or vacant), coastal
Natural areas	Forestry, wetlands

2.4 Results

A total of 124 dens were found during this study with 37 being found in the spring of 2013 and 87 being found in the spring of 2014. Thirty-six of the 87 dens found in 2014 were dens that were surveyed the previous year. Of the 37 dens found in 2013, 32 showed signs of occupation and 5 were determined to be unoccupied. In 2014, 76 of the 87 dens were deemed occupied. A significant difference existed between the elevations of the primary entrances in occupied dens found in 2013 (56.31 cm; two-tailed t-test; $n = 32$; $p < 0.015$) in comparison to occupied dens found in 2014 (77.92 cm; two-tailed t-test; $n = 77$; $p < 0.05$). The majority of the dens (49% for 2013 and 48% for 2014) in Charlottetown had a primary entrance that faced in a southern (S, SW or SE) direction. Vegetation preference within 10 m of den sites was largely long grass (51% for 2013 and 45% for 2014) (Figures 2.3 and 2.4). Significant differences also existed between den descriptors of residential den sites (within 5 m of human infrastructure, $n = 32$) and non-residential den sites (located in more natural areas; $n = 92$) in entrance height, entrance width and elevation of the primary entrance (two-tailed t-test; $p < 0.001$).

A total of 98 distinctive den site locations were observed over the two-year-span with 198 pseudo-absent den locations generated for logistic regression modelling (Figure 2.5). High correlations existed between roads and buildings ($r = 0.851$, $p < 0.05$), as well as unspecified water and brackish water ($r = 0.699$, $p < 0.05$) and unspecified water and non-brackish water sources ($r = 0.5509$, $p < 0.05$) (Table 2.5 (A)). Thus the variables roads and unspecified water sources were eliminated from further analysis. Pearson's correlation analysis of land use variables determined that moderate to strong correlations ($r > 0.4$) existed between areas of high human use and all other land use types (agriculture $r = -0.45$, natural areas $r = -0.45$ and areas of low human use $r = -6.32$; Table

2.5 (B)). Areas of high human were therefore excluded from our logistic regression model.

For land use analysis, three different buffer zone sizes around den sites were considered: 50m, 100m and 150m. Unconditional logistic regressions as well as the Akaike Information Criterion (AIC) determined that the 50 m buffer for each of the land use variables fit the observed data the best (Table 2.6). Therefore, only the 50 m buffer was considered for further analysis with the dataset.

Zonal statistics in QGIS determined the occurrence of each land use type within the 50m buffer for both actual and pseudo-absent den sites (Table 2.7). Significant differences were found between actual and pseudo-absent den sites in regards to the presence of both natural areas ($p < 0.001$) and low human use areas ($p < 0.001$) within the 50 m buffer (Fisher's exact test, actual den ($n = 98$), pseudo absent den ($n = 198$).

Table 2.2. Den characteristics of occupied and unoccupied den sites of Charlottetown, measured during the spring of 2013 and 2014.

Year	Den Feature	Mean	St. Dev	Median	Range
			Occupied (n= 32)		
2013	Elevation of Primary Entrance (cm)	56.31	± 141.25	0.00	(0-790)
	Entrance Height (cm)	23.93	± 6.95	23.50	(11-66)
	Entrance Width (cm)	27.26	± 7.83	26.00	(14-60)
	Number of Entrances	4.29	± 3.21	4.00	(1-12)
			Unoccupied (n=5)		
	Elevation of Primary Entrance (cm)	75.2	± 148.36	0.00	(0-340)
	Entrance Height (cm)	24.43	± 6.22	24.00	(15-30)
	Entrance Width (cm)	29.93	± 8.36	26.50	(19-46)
	Number of Entrances	2.80	± 0.84	3.00	(2-4)
			Occupied (n=77)		
2014	Elevation of Primary Entrance (cm)	77.92	± 87.17	50	(0-300)
	Entrance Height (cm)	24.19	± 6.83	23	(8-58)
	Entrance Width (cm)	28.07	± 8.16	26	(11-62)
	Number of Entrances	4.01	± 3.53	3	(1-22)
			Unoccupied (n=10)		
	Elevation of Primary Entrance (cm)	21	± 29.6	0	(0-80)
	Entrance Height (cm)	22.91	± 6.62	23.5	(8-35)
	Entrance Width (cm)	27.91	± 5.67	28	(11-39)
	Number of Entrances	2.2	± 1.54	2	(1-6)

Table 2.3. Den characteristics of dens located in residential areas (within 5 m of human infrastructure) as well as dens located in non-residential areas (more natural settings) of Charlottetown, measured during the spring of 2013 and 2014.

Den Feature	Mean	St. Dev	Median	Range
		Residential dens (n=32)		
Elevation of Primary Entrance (cm)	26.43	± 69.77	0.00	(0-340)
Entrance Height (cm)	20.04	± 7.82	18.00	(8-58)
Entrance Width (cm)	31.11	± 9.29	31.00	(11-62)
Number of Entrances	3.31	± 1.40	3.00	(1-8)
		Non-residential dens (n=92)		
Elevation of Primary Entrance (cm)	81.32	± 112.09	50.00	(0-790)
Entrance Height (cm)	25.28	± 5.96	25.00	(14-66)
Entrance Width (cm)	26.91	± 7.18	25.00	(22-44)
Number of Entrances	3.98	± 3.28	3.00	(1-15)

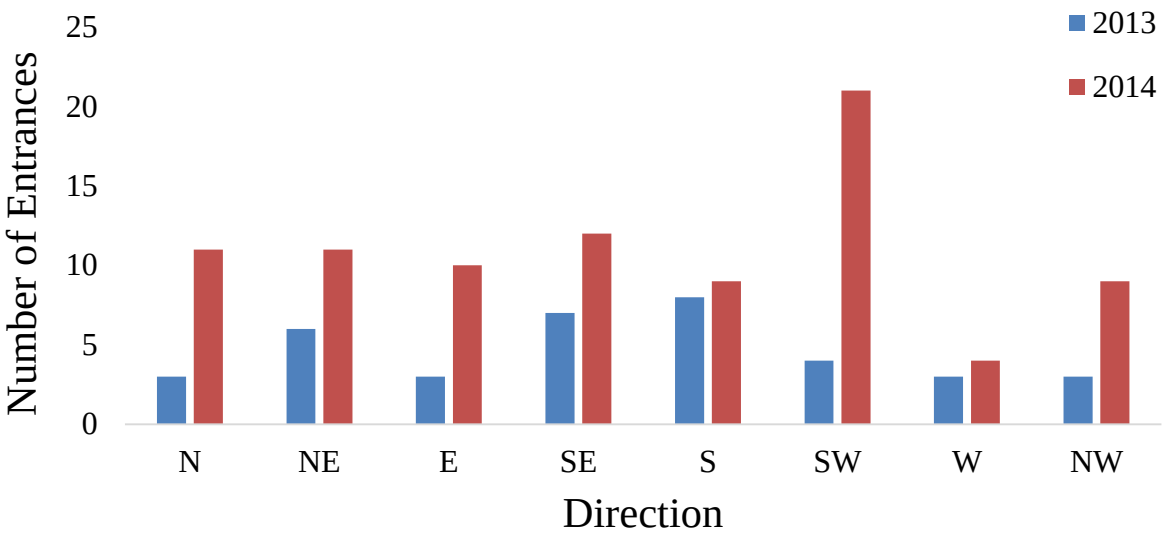

Figure 2.3. Direction of primary entrances for den sites found in 2013 and 2014 in Charlottetown, PEI (2013 n=37 2014 n= 87) N= North, NE = North East, E = East, SE= South East, S = South, SW = South West, W = West, NW = North West.

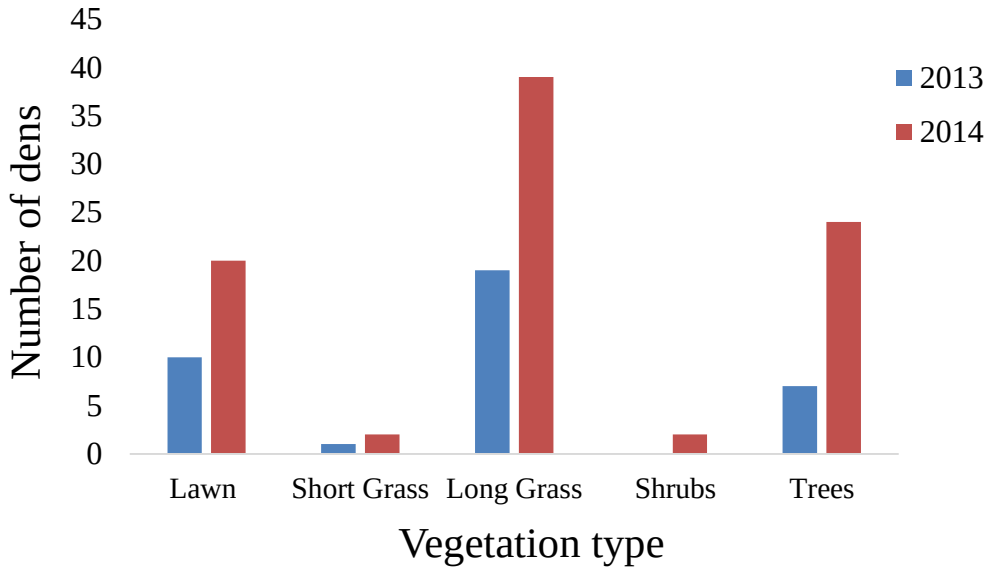

Figure 2.4. Dominant vegetation type within 10 m of den sites in 2013 and 2014 in Charlottetown, PEI (2013 n=37, 2014 n=87).

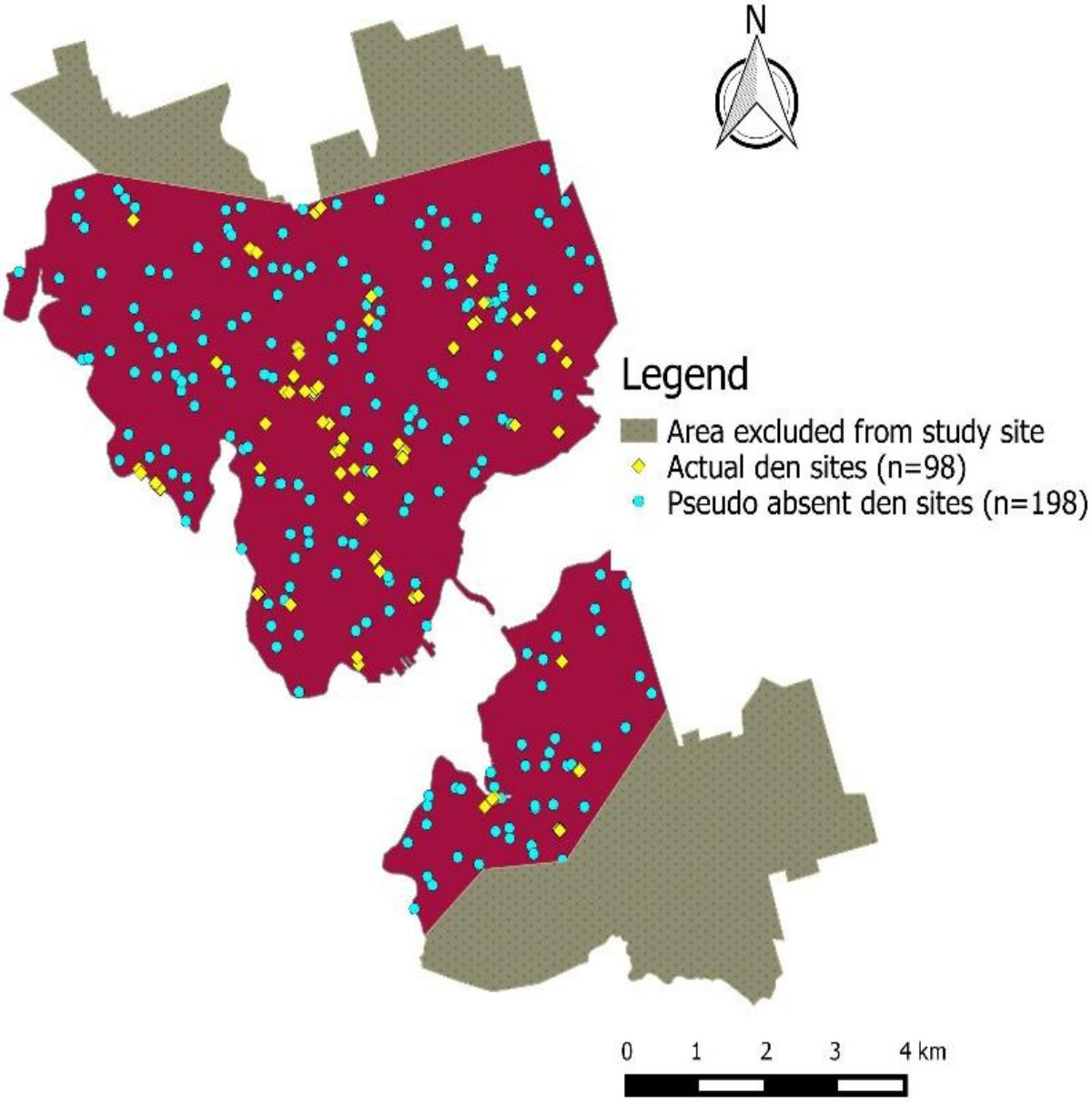

Figure 2.5. A map of Charlotteown depicting the locations of acutal den sites as well as those generated by QGIS that were used as pseudo-absent den sites. Grey areas were excluded from this study due to lack of access and/or lack of fox sightings reported in these areas.

Table 2.4. Distances from actual and control den sites to nearest road, building, water source (unspecified), brackish water source and non-brackish water source.

Distance to Nearest	Actual Den (n=98)			
	Mean (m)	Std. Dev	Median (m)	Range (m)
Brackish Water	897.80	± 635.3	932.90	1 - 2793.7
Building	120.00	± 93.9	92.00	5 - 485.5
Non-Brackish Water	464.80	± 371.9	375.20	1 - 1468.4
Road	95.90	± 77.1	74.40	1 - 391.1
	Control Den (n=198)			
Brackish Water	919.50	± 639	799.70	1 -2687.2
Building	83.70	± 92.8	40.50	1.6 - 444.5
Non-Brackish Water	516.90	± 336.1	450.60	1 - 1596.9
Road	70.60	± 81.8	37.80	1 - 454.7

The environmental predictors included in the final logistic regression model were distance to roads and the presence of natural areas and low human use within the 50m buffers around den sites. Overall, there existed a highly significant interaction between areas of low human use and natural areas ($p < 0.001$; Table 2.8), indicating that the effect of human use on the probability of finding dens, depends on the natural areas available. This model also detected a non-significant trend between the presence of dens and the distance travelled away from roads ($p = 0.061$; Table 2.8).

The distribution of distances from points generated every 5m throughout the study site to the nearest road has a range of 0-819 m with 25% of the points existing 19.8 m from a road, 50 % of the points existing 45.2 m from a road and 75% of the generated points existing 105 m with a mean distance of 79.4 m (Figure 2.4.3). This indicates that den site locations are not limited to a distance of 100 m away from roads, based on the structure of Charlottetown, and that foxes are demonstrating some degree of selection for this distance.

Table 2.5. Pearson's correlation matrices for (A) distance variables used in this study (B) land use variables (agriculture, natural areas, low human use areas and high human use areas) used in this study Values in bold are deemed to be highly correlated ($r > 0.4$) and therefore excluded from further analysis.

(A)

Distance to	Roads	Buildings	Water (unspecified)	Non-Brackish Water	Brackish Water
Roads	1				
Buildings	**0.851**	1			
Water	-0.24	-0.2091	1		
Non-Brackish Water	-0.19	-0.1921	**0.6985**	1	
Brackish Water	-0.05	-0.0026*	**0.5509**	0.1696	1

*$p < 0.05$

(B)

Area	Agriculture	Natural	Low human-use	High human-use
Agriculture	1			
Natural areas	-0.0612	1		
Low human use	-0.1081	-0.0317	1	
High human use	**-0.4519**	**-0.4511**	**-0.6324**	1

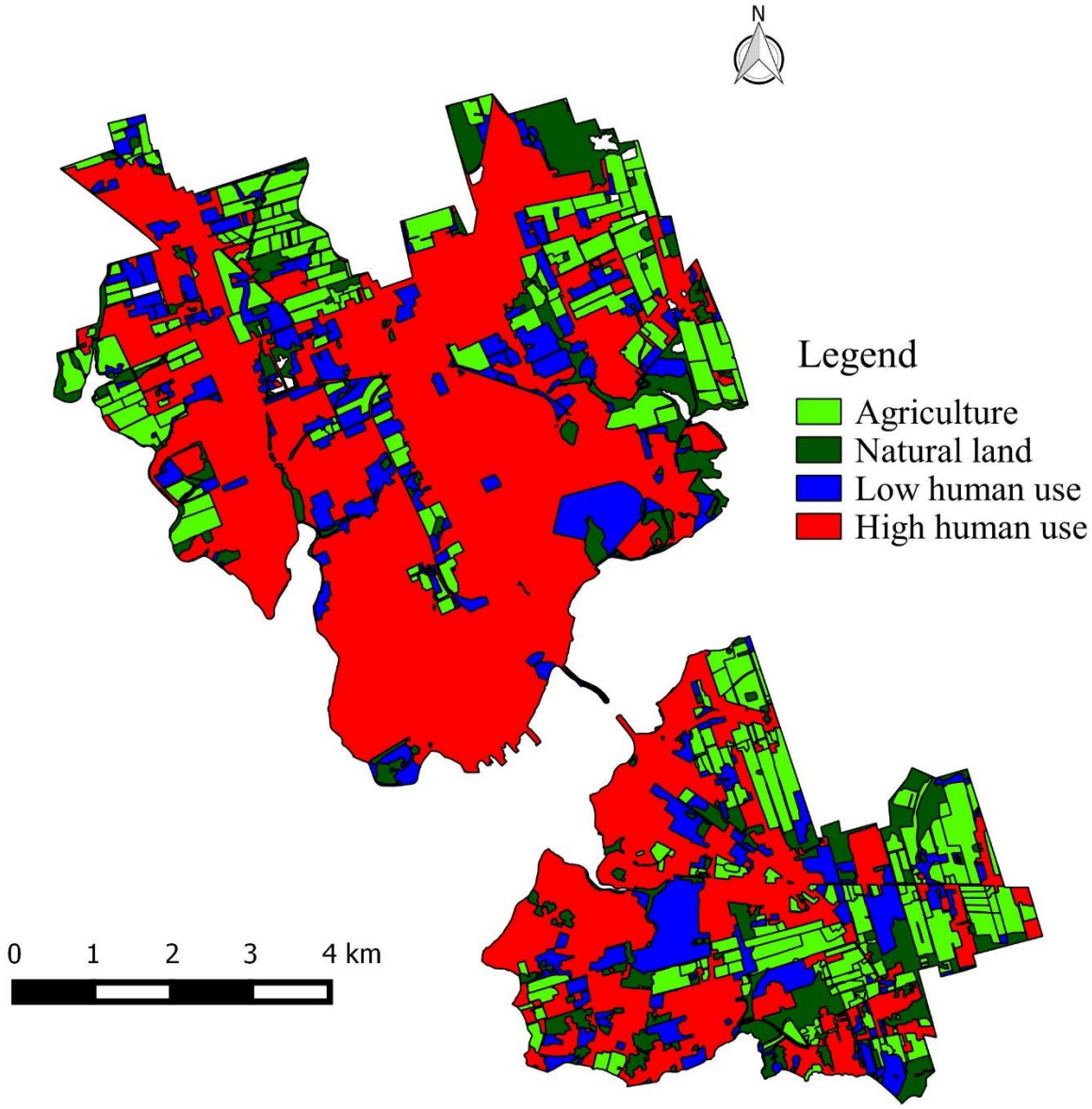

Figure 2.6. Modified land use classification of Charlottetown PEI, used for this study exhibiting Agricultural land, natural land and areas of low human use and high human use.

Table 2.6. Results from unconditional logistic regression (with presence/absence of den sites as the outcome) and AIC analysis to determine which buffer zone fit the data best for each land use variable. Values in bold indicate the lowest AIC values with the best fit (n =296, df = 6).

Model	AIC
Agriculture	
50 m buffer	**372.54**
100 m buffer	375.07
150 m buffer	377.76
Natural	
50 m buffer	**365.44**
100 m buffer	368.86
150 m buffer	371.96
Low human use	
50 m buffer	**360.68**
100 m buffer	364.99
150 m buffer	370.21
High human use	
50 m buffer	**361.83**
100 m buffer	367.13
150 m buffer	370.33

Table 2.7. Presence of land use types (agriculture, natural areas, low human use and high human use) within 50 m buffers of fox den sites (both actual and pseudo-absent) in Charlottetown.

Land use	Actual den (n=98)		Pseudo-absent den (n=198)		Fisher's Exact
	Present (%)	Absent (%)	Present (%)	Absent (%)	p
Agriculture	14 (15)	84 (85)	42 (21)	156 (79)	0.160
Natural areas	39 (40)	59 (60)	28 (14)	170 (86)	<0.001
[a]Low human use	49 (50)	49 (50)	44 (22)	154 (78)	<0.001
[b]High human use	69 (70)	29 (30)	155 (78)	43 (22)	0.151

[a] recreational, non-evident and coastal lands in Charlottetown
[b] urban, residential, transportation, commercial, industrial and institutional lands in Charlottetown.

Table 2.8. Results of Logistic Regression model predicting the likelihood of occurrence of red fox dens in Charlottetown (n=296) based on the distance travelled away from roads as well as the presence of natural areas and low human use areas within a 50 m buffer of den site.

Predictor	Coefficient	Odds Ratio	95% Confidence Interval	p
Distance to road (≤100m)	0.095	1.099	0.995, 1.216	0.061
Distance to roads (>100m)	-0.044	0.956	0.902, 1.014	0.136
Interaction				< 0.001
No human use and no nature areas		Baseline		
Low human use only	1.522	4.582	2.288, 9.175	< 0.001
Natural areas only	1.809	6.103	2.675, 13.921	< 0.001
Both natural areas and low human use	1.598	4.796	1.968, 11.692	0.001
Intercept	-1.956			

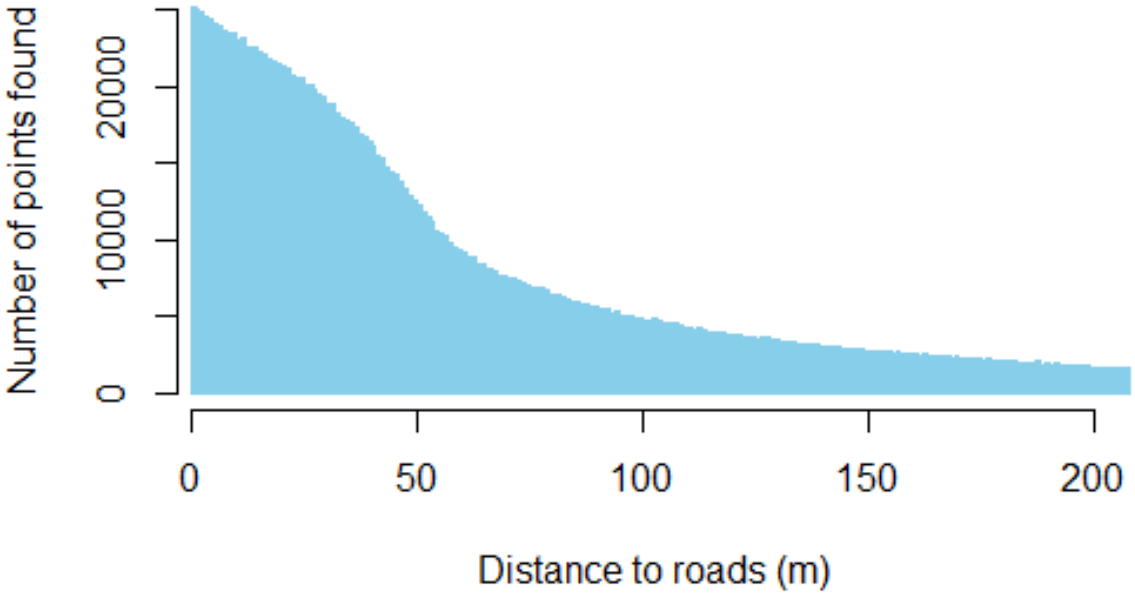

Figure 2.7. A histogram showing the distribution of distances from uniform points generated at 5 m intervals within Charlottetown to the nearest road. This metric was used to determine the farthest distances possible away from roads that foxes could potentially construct den sites.

2.5 Discussion

Foxes of PEI have demonstrated a high degree of adaptability with regards to den site selection and den structure within the province's largest urban center of Charlottetown. Although they prefer to den in areas with less human disturbance, they quite often will utilize human infrastructure and residential properties when necessary. Seventy-one percent of dens surveyed in Charlottetown were located in settings that reflect rural fox habitats such as fields, wooded areas and banks of coastal lands, while 21 percent were located in residential areas within 5 m of human infrastructure. The lack of regular human disturbance has shown to be an important factor in den site selection in urban areas around the globe including; London (Harris 1977), Toronto (Adkins and Stott 1998) and Melbourne (Marks and Bloomfield 2006).

Despite the continued success of red foxes in urban areas, there remains to be a general lack of information regarding urban den site selection in recent literature. To our knowledge, one of the only studies existing, focusing on urban den site selection was conducted by Marks and Bloomfield (2006), in Melbourne, Australia. Through similar survey techniques, Marks and Bloomfield (2006) located 72 natal dens in a 20 km radius area (~ 1260 km^2) within Melbourne. In comparison, with Charlottetown being a much smaller city, 98 den sites were found within a survey area with a radius of approximately 6 km (~ 113 km^2). Although more den sites were found within Charlottetown, the study in Melbourne was exclusively looking for natal den sites and therefore may have been an underestimation of the total number of dens within an urban center of that size. Natal dens are defined as dens in which the kits are born and spend the majority of their early lives (Henry 1986). Non-natal dens may be any other den in which the kits were not born.

An example of a non-natal den may be an alternative den located a short distance from the natal den as it is common for red foxes to excavate more than one den so that in the event of a threat they may have an additional safe area to rear their young. We were interested in both natal and non-natal dens as we wanted examine what habitat preferences foxes demonstrated, not only for giving birth, but also throughout the entirety of a young fox's upbringing and thus our findings should be viewed more generally.

It is possible that the high number of fox dens in Charlottetown could represent a more dense urban fox population. This may be the case as foxes in Charlottetown began to colonize urban areas following the migration and establishment of eastern coyote (*Canis latrans*) populations on PEI. Red foxes have been known to avoid areas where coyotes are present to circumvent competition with the larger canine (Harrison et al. 1989, Sargeant et al. 1987, Voigt and Earle 1983). In Australia, similar spatial relationships have been observed between foxes and dingoes (*Canis lupus dingo*) (Thompsen 1983, Smith and Quin 1996, McRae 2004, Newsome et al. 2001, Glen et al. 2007). The lower number of fox dens in Melbourne could be the result of the absence of dingoes in surrounding rural areas. With no major competitors, foxes would likely still occupy this more rural niche. In fact, a study done by Newsome et al. (2001) measured the abundance of red foxes in areas of south-eastern Australia, which excludes dingoes, and found that indices of fox abundance were 7.1 to 20.6 times higher in these areas compared to areas where dingoes are present (Glen et al. 2007).

In our study design, the citizen science methodology that was used to primarily seek out den locations within Charlottetown was very successful. Information submitted by the public accounted for 36 % of the den sites found within the city. This

methodology allowed us to gather large amounts of data, at a rapid pace with very little associated cost. Citizen science has proven to be successful in many branches of urban wildlife ecology including: presence/absence surveys (Weckel 2010), tracking infectious disease (Crowl et al. 2008), phenological studies (Hickling et al. 2006) and species range shifts. (Lemoine et al. 2007, Zuckerberg et al. 2009). For the purposes of this study, citizen science has effectively helped us establish baseline data on where foxes are being observed in Charlottetown, and more specifically, where dens may be located based on high volumes of observations. One of the main criticisms of using citizen science as a data collection technique is the increased likelihood of error and bias due to the variation in observer quality (Dickinson et al. 2008). This challenge was overcome, however, by visiting every den site location reported by the public in order to confirm den activity based on characteristic evidence of fox dens. In addition to allowing us to collect survey data from private property, using citizen science has also increased interest and awareness surrounding urban foxes in Charlottetown and has given us the opportunity to educate a larger audience on the topic of healthy human-wildlife interactions.

In many parts of the world foxes will modify burrows already excavated by other mammals such as badgers or rabbits (Lloyd 1980, Marks and Bloomfield 2006). This is not the case on PEI, however, as the province lacks additional fossorial mammal species and therefore foxes are required to exhume their own dens. The soil structure of PEI is characterized by a fine sandy loam texture (Government of PEI 2012) and thus is ideal for den excavation due to its water draining capabilities and easy-digging consistency (Soper 1942, Sheldon 1950, Carter et al. 2012). The mean number of entrances per den in Charlottetown is 4 ± 3.21 for occupied den sites and 3 ± 0.84 for unoccupied den sites.

These findings are comparable to a study done in Japan by Uraguchi and Takahashi (1998) who found the average number of entrances to be 3.5 ± 3.6. The number of entrances that a den has can range from only one to more than 20, as multiple den entrances are common to allow for easy escape routes (Sheldon 1950, Murie 1944, Berghout 2000, Carter et al. 2012). Dens sites with high numbers of entrances are generally older dens that have been used in multiple kit-rearing seasons (Nakazono 1987). The simple reason for this being that as a fossorial mammal, the more time spent at a den site or the more individuals that live there, the more likely the foxes are to dig new entrances (Arjo et al. 2003). For both years of the survey, the average entrance dimensions of dens in Charlottetown measured approximately 24 ± 7 cm in height by 27.5 ± 8 cm in width for occupied dens, and 28 ± 7.5 cm by unoccupied den sites. These dimensions are similar to dimensions reported by Storm et al. (1976) and Pils and Martin (1978) from rural studies from the mid-western states, both finding entrance dimensions averages being 28 x 23 cm (Krim et al. 1990). Comparable entrance heights were also recorded for red foxes in northeastern China with wild sites measuring 27.3 ± 8.8 cm (Chung et al. 2015).

Foxes are able to squeeze themselves through holes less than 10 cm in diameter (Harris and Baker 2001), which may be beneficial when utilizing urban infrastructure or, digging dens in soil types that are not ideal for excavation. Some species of fox, such as the kit fox (*Vulpes macrotis*) and the bat-eared fox (*Octocyon megalotis*) will minimize entrance diameter or select den sites with smaller entrances, in order to reduce the potential for predation by larger carnivores (Arjo et al. 2003). Perhaps we would see this trend in rural PEI fox dens in the few areas where coyote and fox territories overlap. In

Charlottetown, however, entrance size may be more comparable to other rural fox den measurements due to the lack of predators found in urban areas.

When comparing den characteristics between dens found in residential areas versus dens found in non-residential areas, significant differences were found in entrance height, entrance width and the elevation of the primary entrance (two-tailed t-test; entrance height, width and elevation of primary entrance in residential dens versus non-residential dens, $p < 0.001$). Residential dens ($n= 32$) tend to have shorter, wider entrances with the elevation of the primary entrance being low to the ground (Table 2.4.2). This is most likely due to these dens being dug under human infrastructure such as backyard sheds, patios and garages. The majority of the dens ($n = 92$) found in Charlottetown were found outside of residential neighborhoods, in areas that reflect more natural habitat. These dens have taller entrances, with the primary entrance being located at a higher elevation. Foxes tend to dig into a slope or a mound for the ease of excavation as well as the enhanced water draining capabilities (Henry 1986, Goszczynski 1999, Goldyn et al. 2003, Uraguchi and Takahashi 1998). Arctic foxes have showed similar preference for elevated mounds of soil as this allowed them to dig their dens above the unfrozen ground of the tundra (Chesemore 1969). It is possible that foxes in PEI would also select den sites based on elevation as many dens are excavated in February and March when the ground is still frozen.

Although it seems that urban foxes still prefer to locate their dens in a more natural setting, den site selection may be heavily influenced by factors such as fox density and resource availability. For example, in the city of Bristol, UK, where fox densities were once the highest in the world, most dens were located under garden sheds

due to a disproportionate amount of natural areas to the number of foxes found here. Following a mange outbreak however, where the fox population underwent a drastic decline, den locations shifted towards more natural sites such as old badger setts (Newman et al. 2003, Soulsbury et al. 2010). Although it is possible that Charlottetown's foxes choose residential neighborhoods to den due to the lack of natural areas available to them, it may also reflect direct and indirect food sources provided by humans. It has been found that in many urban areas, a significant portion of residents may feed foxes (Harris 1981, Lewis et al. 1993, Contesse et al. 2004, Soulsbury et al. 2010). For instance, when fox densities were at their highest in the UK, 10% of homeowners in Bristol were leaving out food for foxes on a daily basis (Baker et al. 2000). Wildlife officials in PEI suggest similar trends are starting to develop within the province as many Charlottetown residents as well as tourists admit to providing the foxes with food (B.Potter and C.Gallison, PEI Dept. of Fish and Wildlife, personal communication). Being opportunistic omnivores, it is not surprising that 27% of den sites were found within residential areas. These reliable and energetically efficient food resources being provided by humans ensure consistent nourishment for prenatal females as well as growing kits.

Directional orientation of primary den entrances were predominately towards the south (49% in 2013 and 48% in 2014). Southern facing fox burrows are common in both arctic and red foxes as documented by (Danilov 1961, Chesemore 1969, Garrot et al. 1983, Dalerum et al. 2002 and Szor et al. 2008). This may be a technique to avoid the prevailing winds and provide enhanced thermal insulation (Prestrud 1992, Nielson et al. 1994). Red foxes in Charlottetown may have developed similar microclimatic selection techniques as an adaptation to cold winter climates of higher latitudes. Most often dens

are dug out in January and February to prepare for the birth of cubs in March where kits will remain underground for the first month of their life (Harris and Baker 2001). These southern facing dens may allow for an increased exposure to sunlight and snow-melting capabilities in the spring. In contrast, however, a study conducted in Shiqu County, China (Wang et al. 2007) recorded predominately west facing entrances for Tibetan fox (*Vulpes ferrilata*) dens in an area in which wind direction was typically form the south west. Thus, it is possible that in regions where wind speed and direction is highly variable, den entrance direction may not be a factor in den site selection. This is not thought to be the case in PEI however, as the predominant wind direction within the Maritime provinces of Canada (including PEI) is west or northwest in winter (Robichaud and Mullock 2002) and thus may play a role in the selection of southerly facing den site locations within Charlottetown.

Vegetation preference within 10 m of the primary entrance was found to be primarily long grass. Long grass is generally attributed to natural areas that are not frequented or maintained by humans. In rural areas and even non-residential areas of cities, this type of vegetation may be important for den camouflage during kit-rearing as well as the abundance of rodents that may be found in this type of habitat. In residential areas of Charlottetown, however, den camouflage does not seem to be a priority as in most cases, short grass of lawns is the only nearby vegetation type. Foxes in urban areas have known to become habituated to human presence and even associate humans with easily attainable food resulting in very "tame" behaviour (Baker et al. 2000, Baker et al. 2004). For example, photos captured by a trail camera at a residential den in Charlottetown during the spring of 2013, documented a family of foxes who would

utilize the yard minutes after humans occupied this space. In fact, the only time the foxes would flee is when the barn in which the den was under was being entered/exited (Lambe 2013, unpublished data).

In this study, we found that 32 dens were located in residential properties in close association with human infrastructures (e.g., under backyard sheds and patios). According to officials with the PEI Department of Forests, Fish and Wildlife, the increased presence of fox dens in these locations has also lead to an increase in complaints from Charlottetown residents (B. Potter and C. Gallison 2013, personal communication). Grievances surrounding den sites on residential property stem from the multitude of old shoes, stolen dog toys, bones and feces that are associated with young foxes; or from fear that the fox may become aggressive towards small children or pets. In terms of successful mitigation, it is important to understand how foxes select dens at both a small and large spatial scale in urban areas in order to prevent the unwanted den sites and maintain a harmonious fox-human relationship.

It is also important to consider major structural components of urban landscapes (i.e.; roads and buildings) at larger spatial scales when investigating urban ecology. Dens in Charlottetown were found a mean distance 95.9 ± 77.1 m away from roads. Results from our logistic regression model also suggest that there is a relationship between distance from roads and the occurrence of den sites, where you are more likely to find a den, the farther you travel away from roads. This relationship shifts, however, once you travel beyond 100 m, where after, the likelihood of finding a den decreases. These findings advocate that foxes in Charlottetown are demonstrating a biological preference for denning habitats away from roads. Selecting den sites away from roads and high

traffic areas may reduce the noise disturbance associated with such areas as well as limit vehicular mortalities of young in the spring.

Spatial analysis was also conducted to investigate whether this distance (~ 100 m) was indeed biological selection, or if it was a merely a product of the structure of Charlottetown (i.e: there was no available land more than 100 m away from roads within the city, Table 2.3.5). From this we determined that although there is in fact land available at distances >100 m from roads, the foxes are actively selecting areas close to the 100 m distance for denning habitat. This could mean that although foxes choose to be a distance away from the roads for denning success, perhaps they also benefit from having easy access to roadways for the purposes of efficient foraging or direct routes to accessible resources. Rosatte and Allan (2009), for instance, observed foxes in metropolitan Toronto frequently crossing or travelling along roads to access nearby green spaces. In Charlottetown, many residents are known to provide food daily to foxes and therefore roads may offer a direct path to easy and reliable sources of energy. A previous study conducted on PEI by Silva et al. (2009) reported that foxes in the Prince Edward Island National Park select roadways as preferred habitat in the spring and summer due to the quantity of people who provide them with food. It is likely that dens existed close to these areas as well. Furthermore, similar outcomes were observed in a region of North Africa where aggregations of red fox den sites were influenced by distance to roads and profitable foraging opportunities (Dell'Arte and Leonardi 2007).

When in natural areas or areas of low human-use in Charlottetown, the odds of encountering a fox den increased 4-6 times compared to regions that do not contain either of these land use types, possibly suggesting that foxes prefer one or both of these land use

types for denning habitat. Within an urban center, these are the spaces that are the least frequented by humans, again, reinforcing that avoidance of humans is an important determinant in den site selection. Although, for example, human traffic increases throughout the summer months on golf courses, urban foxes have been known to use these areas more actively at night when humans are absent (Adkins and Stott 1998). This preference is also observed by red foxes in Melbourne Australia where 61% of natal fox dens within the city were located in areas where public access was limited or restricted to daylight hours only (Marks and Bloomfield 2006). In addition to lack of human disturbance, natural areas and areas of low-human use are less likely to be exposed to domestic dogs. A study done in the United Kingdom (Harris 1981) demonstrates the tendencies of red foxes to avoid denning on properties with domestic dogs due to potential mortality risks to cubs. Unpublished results from trail cameras placed at den sites in Charlottetown (H.Lambe, 2013-2014) support these findings as photos of only two domestic dogs were captured near fox dens in natural areas and in both cases the dogs were on a leash and under control by their owner.

In conclusion, the physical measurements of den sites in Charlottetown are comparable to other studies worldwide. The distribution of urban den sites in Charlottetown appears to be influenced by lack of direct human disturbance and access to profitable foraging grounds. Kit-rearing is a very energetically expensive period in an adult fox's life. They must provide multiple young with substantial amounts food as well as select a home that provides shelter and protection for them during time of parental absence. Natural areas and areas of low human-use generally offer a greater abundance of

vegetative shelter suitable for camouflage as well as a more constant supply of rodents, birds and amphibians based on the variety of habitats found here.

Although we have confirmed the locations of 98 distinct den sites in Charlottetown, it is important to note that we are not claiming this is a comprehensive study of the distribution of den sites as survey bias may exist due to areas accessible to researchers. Urban areas, such as this, will continue to evoke multiple challenges when sampling wildlife due to the multitude of private properties found here. However, the application of citizen science as well as the adaptation of species distribution models to den site data has helped us determine factors to identify potential den sites in unreachable areas, based on the environmental preferences exhibited in observed den site locations. Species distribution models have recently become more common in ecological studies and have the potential to become an invaluable tool in urban management and conservation strategies. Potential examples of such strategies could include disease outbreak control, or the protection and development of natural areas that are highly used by the foxes. With a concrete knowledge of where foxes prefer to excavate den sites and why, it may be possible to predict potential den locations and prepare residential properties according to individual feelings about foxes. Keeping wildlife at a distance, within urban areas, and the knowledge as to what factors may influence this, will in turn lead to a harmonic existence between humans and foxes.

During this study we discovered many aspects of urban den site ecology that could not be covered by the scope of this project. We do believe, however, that future studies are pertinent for the comprehensive understanding of den site selection within urban areas of PEI. Some recommendations would be first, to conduct annual surveys of

dens in the city. We encountered a number of dens over the two-year study period which were used in multiple years, and others that appeared to be used for a single breeding period. Although the majority of foxes are clearly selecting for particular types of habitat within the city, they have also exhibited a high level of adaptability. A better understanding of why they remain in one area versus why they might leave another is important for management tactics should they need to be implemented. Secondly, it may be important to differentiate between natal and non-natal dens as natal dens seem to cause the most problems on residential properties due to the amount of mess and noise associated with young foxes. Determining whether or not habitat requirements are different for each type of den, and how and when each type of den is used may provide a better understanding of the overall behavior in urban environments.

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Chapter 3

Habitat selection and home range patterns of urban red foxes (*Vulpes vulpes*) on Prince Edward Island, Canada

3.1 Abstract

The red fox is known to be one of most successful urban canid species due its adaptive nature and opportunistic diet. Like many other wild canine species, foxes establish and defend home ranges to ensure they can maintain adequate resources for maximum reproductive success in both rural and urban environments. Information regarding home range and habitat selection is imperative for successful wildlife management strategies within urban areas in terms of proactive control measures and the conservation of important fox habitat. The main goal of this study was to investigate patterns of home range size and habitat selection of foxes within urban Charlottetown (Prince Edward Island, Canada) and examine the roles of seasons and gender. Data were collected via GPS collars over three seasons (summer, fall, winter) between August 2013 and October 2014. Home range size and habitat selection were examined for six foxes (two males, four females). Using minimum convex polygon we found that home ranges of captured red fox ranged from 88 – 1406 ha. Differences in home range size may be

attributed to the availability and accessibility of urban resources with larger ranges being more common in winter due to the challenges associated with snow cover. Home range size may also vary based on intersexual behaviours such as mating and kit-rearing. Overall, the home range sizes of foxes in Charlottetown are relatively large compared to data collected in rural PEI and from urban areas in other cities worldwide and thus it is possible that foxes may perceive urban areas on PEI as similar to rural or suburban environments. Foxes in Charlottetown positively selected for areas less-disturbed by humans such as natural lands, agricultural areas and regions of low human-use. This further suggests that resource distribution plays a key role in urban fox ecology as these areas are likely to contain a greater abundance of natural food sources, vegetative cover and potential denning locations.

3.2 Introduction

The opportunistic nature of red foxes as well as their generalist diet preferences have allowed the species to successfully colonize urban areas worldwide, e.g. London (Soulsbury et al. 2010), Bristol (Harris and Baker 2001), Toronto (Adkins and Stott 1998), Melbourne (Marks and Bloomfield 1999) and Zurich (Contesse et al. 2004)). Like other wild canids, foxes establish and defend home ranges to ensure they can maintain adequate resources (e.g., food, mates and denning habitat) for maximum reproductive success in both rural and urban environments. (Ables 1969, Macdonald 1981, Voigt and Macdonald 1984, Voigt 1987, Goszczynski 2002).

On Prince Edward Island (hereafter PEI), foxes began to extend their ranges to urban areas in response to the immigration and establishment of the Eastern coyote (*Canis latrans*) in the 1980's. Since then, foxes have continued to successfully adapt to

PEI's urban environments. Evidence suggests that urban fox populations on PEI have increased over the last decade (B. Potter and C. Gallison, personal communication, PEI Department of Forests, Fisheries and Wildlife). To date, minimal research has focused on red foxes on PEI and existing studies have examined only foxes in rural areas. As urban carnivores such as red foxes, striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*) and coyotes (*Canis latrans*) become more abundant in urban areas, so does the potential for increased levels of conflict with humans (Thouless and Sakwa 1995, Torres et al. 1996, Woodroffe 2000, Naughon-Treves et al. 2003, Treves and Karanth 2003, Gehrt 2004). Within urban areas, such conflicts include nuisance issues such as property damage (denning foxes), noise (raccoons) or odors (skunks). They also may stem from potential public health issues involving urban carnivores, such as disease transmission and the possibility of physical attacks on domestic pets and people (Gehrt 2004). Thus, if the number of foxes continues to increase in urban areas of PEI, so does the probability of conflict between humans and foxes and therefore a greater need to understand habitat selection within Charlottetown in order to identify areas where potential conflicts may occur.

It has been recognized that individual wildlife species respond to their environment at a unique range of spatial scales, and thus multi-scale approaches to examining species-habitat relationships are essential (Levin 1992, Bissonette 1997, Cushman and McGarigal 2004, Graf et al. 2005). This is also true for urban species, such as the red fox. For instance, at a large spatial scale an animal selects an area that is able to support them for a prolonged period of time, known as their home range. At a smaller scale, the animal selects a core-use area, which is defined as an area of an animal's home

range that is more frequently utilized than others and most likely contain home-sites, refuges, courtship opportunities and the most reliable sources of food (Burt 1943, Kaufmann 1962, Ewer 1968, Samuel et al. 1985, Levin et al. 2009).

To our knowledge, despite the success of foxes in urban areas, very few studies have been conducted in North America on urban home range and habitat selection of the red fox. Recent literature regarding urban carnivores in North America and Europe, suggests that in many cases, the home range size of urban carnivore decreases in comparison to the home range size of their rural equivalents as a consequence of urban habitat fragmentation and the scarcity of natural green spaces (Sálek et al. 2014, Iossa et al 2010, Bateman and Fleming 2012). More specifically, abundant seasonal food resources, decreased predation and protection from hunting are largely responsible for increased survival rates in urban areas leading to higher population densities and decreased range sizes (Bateman and Fleming 2012). Previous studies conducted on red foxes confirm this pattern with urban home range sizes recorded at 29.6 ha in Melbourne (Marks and Bloomfield 2006), 38.8 ha Oxford (Doncaster and Macdonald 1991) and 52 ha in Toronto (Adkins and Stott 1998) in comparison to home ranges measuring up to 3400 ha in rural landscapes of Ontario (Voigt 1987, Geffen et al. 1992). The large amount of variation that exists within the home range sizes of red foxes, both rural and urban may also be resultant of factors specific to each study area including: the duration of the study, methodologies used, geographic features, demographics of the population studied, the distribution of resources, mortality risks and the proportion of suitable habitat available (Červinka et al. 2013, Sálek et al. 2014).

Home range size may also fluctuate seasonally in response to resource availability and reproductive behaviour (Borger et al. 2006, Kjellander et al. 2004, Hewison et al. 1998). For instance, home range sizes of many species are known to be smaller when food is readily available, and may be larger when food is more difficult to find as they are not required to travel as far to acquire sufficient resources. For canids living in northern latitudes, (e.g. wolves) snow accumulation during the winter has been shown to alter home range size, as primary productivity of an area is reduced which in turn decreases prey densities (Jedrzejewski et al. 2007, Mattisson et al. 2013). In addition to resource availability, the reproductive status of an individual may also be responsible for changes in home range size. This effect is typically more pronounced in females as behavioural changes (along with resulting home range sizes) are responses to energetic requirements, mobility and increased predation risks associated with rearing young (Tufto et al. 1996, Grignolio et al. 2007, Long et al. 2009, van Beest et al. 2011).

Habitat selection occurs within a home range when an animal chooses to use a particular habitat type disproportionately to its availability (Johnson 1980). For example, natural areas may only exist in small patches within an urban environment (i.e., preserved land, parks). However, many species of wildlife may spend most of their time in these small patches despite the lack of space, due to key resources such as cover and food found within these areas. Habitat selection can also vary based on factors such as predation risk, localized food availability and reproductive behaviours. For many organisms, it is presumed that choosing to forage within specific resource patches is somewhat dependent upon the associated risk of predation (Brown 1988, Lima and Dill 1990, Brown et al. 1999, Morris 2003). Elk, for example have been known to alter their

preference for aspen stands and forest in relation to the distributions patterns of wolves in the area (Creel et al. 2005, Fortin et al. 2005, Fortin et al. 2009). In addition to predation risk, habitat selection is also based upon the types and quality of resources available, and the extent to which these resources are utilized by conspecific and interspecific individuals (Fretwell and Lucas 1970, Rosenzweig 1981, Morris 1988, Morris 2003).

Intraspecific differences in habitat selection are also known to exist between males and females of mammalian species based on gender distinct selection pressures, age and reproductive roles (Wilson 1975, Crook et al. 1976, Eisenberg 1981, Gehrt and Fritzell 1998). For example, adult female selection pressures are commonly linked to reproductive success and the ability to exploit resources needed to nurture young, both in-utero and after giving birth, whereas the reproductive success of adult males is generally linked to the ability to successfully find and mate with females (Wilson 1975, Rowell 1988, Clutton-Brock 1989, Gehrt and Fritzell 1998). These gender differences can also affect the size and location of home range boundaries generally resulting in larger home ranges exhibited by males. A clear demonstration of such gender differences is evident in a study conducted by Gehrt and Fritzell (1998) whereby the spatial organization of raccoons (*Procyon lotor*) showed several females whose home ranges overlap in areas of high resource availability, whereas the home ranges of males only overlapped in areas of high female distribution.

Despite seasonality or gender, one of the most obvious challenges that exist for urban dwelling species is the high degree of habitat fragmentation present in urban areas. Habitat fragmentation, as defined by Lord and Norton (1990), is the breaking up of a large intact area of vegetation into smaller units. Although natural areas can be subject to

habitat fragmentation, this phenomenon is more pronounced in urban areas due to major anthropogenic infrastructure such as roads, commercial buildings and residential areas. Fragmentation effects can vary based on the unique spatial organization and population densities of different cities, but the fragmented patches within cities usually become smaller and more isolated towards the urban centre (Cousins 1982, Dickman 1987). The lack of connectivity between green spaces such as parks, woodlands and large backyards makes movement through a city increasingly difficult for urban carnivores. Additionally, habitat selection may be influenced by human disturbance, street lighting, noise pollution, habitat loss and modification in which wildlife are regularly exposed to in urban area which may cause animals to adjust their behaviour, ecology and physiology in order to adapt to such urban pressures (Luniak 2004, Ditchkoff et al. 2006, Dudus et al. 2014). The ability to move safely between resource patches becomes increasingly important in urban areas as it assures access to food and shelter, refuge from predators, as well as plays a major role in dispersal abilities and over all genetic diversity (Taylor at al. 2006, Braaker et al. 2014).

With the increasing success of carnivores in urban areas, it is imperative to gain a deeper understanding of how these species are using spaces that are also highly populated by humans in order to prevent conflict as well as the spread of disease (Bateman and Fleming 2012, Soulsbury et al. 2010). Human attitudes towards red foxes vary worldwide, mainly depending upon the probability of disease transmission between wildlife and humans. In many regions, for instance, foxes are a vector for the rabies virus. In these areas it is common for residents to perceive foxes as a nuisance species. On PEI, however, rabies is currently not prevalent so foxes are not regarded as a threat. In fact,

many people enjoy having the foxes around and actively participate in feeding them. It is possible, however, for humans and domestic pets to contract other serious diseases and parasites from foxes on PEI, such as canine round worm (*Toxocara canis*). This parasite is usually contracted by coming in contact with fox feces (G. Conboy, Atlantic Veterinary College, personal communication). For this reason the practice of fox feeding is likely to lead to foxes spending more time on residential properties, thus increasing the amount of feces present and consequently increasing the potential risk of parasite transmission.

Fox feeding has also been reported in the city of Bristol (UK) where as much as 10% of households in any given neighborhood were consistently providing food for foxes (Harris and Baker 2001). In fact, in one neighborhood, a strong relationship was detected between the amount of food being left out, and the number of adult foxes that the area could potentially support (Harris and Baker 2001). This is one example of how human activities are capable of affecting where foxes choose to spend their time as well as the number of foxes present in a particular area.

Information concerning home range, habitat selection and the core-use of urban carnivores such as red foxes is especially imperative to future conservation and management strategies for several reasons: 1) this information may be imperative should control measures need to be implemented by wildlife officials in the case of a zoonotic disease outbreak (e.g. rabies virus) and 2) by contributing to active management within the city to protect and expand important fox habitat in an effort to guide potential habitat use by foxes. Furthermore, developing a greater understanding of how foxes perceive and utilize the urban environment allows us to educate the general public on key topics such

as: the urban ecology of red foxes, the negative implications associated with feeding wildlife and how to humanely prevent the use of residential property by foxes, which may in turn limit the number of negative fox-human interactions.

The main goal of this study, was to investigate home range sizes and patterns of habitat selection of red foxes within Charlottetown. In addition, we wanted to examine the effects of gender and season on home range and habitat selection. We hypothesize male foxes will demonstrate larger home range sizes than females based on gender roles and resource distribution. We also hypothsize that foxes collared during the winter will maintain larger home ranges due to the challenges associated with obtaining resources under snow cover. In addition, we expect that foxes in Charlottetown will actively select for more natural areas within the urban matrix despite gender or seasonality, with areas of high human use being important due to the distribution and abundance of anthropogenic resources.

3.3 Materials and Methods

3.3.1 Study Area

Charlottetown is the capital city of Prince Edward Island (PEI), as well as the largest urban area in the province with a population of 34,560 (PEI Statistics Bureau 2014) and an area of 44.3 km^2 (PEI Department of Environment, Energy & Forestry, 2010). The Charlottetown area encompasses land along the southern shore of the province and is constrained by the Hillsborough and the North River with much of the city being exposed to the Charlottetown Harbour. Urban development is prominent along the waterfront with suburban areas stretching to the east, north and west with pockets of

commercial development towards the northern perimeter. Along with urban and suburban development, Charlottetown boasts over 158 parks and green spaces that make up an area over 2.2 km^2 throughout the city (City of Charlottetown 2014). Another prominent landscape feature in the city is the 0.65 km^2 of agricultural land belonging to an Agriculture Canada crops and livestock research station (Agriculture Canada 2014).

3.3.2 Live Trapping and Handling

Trapping efforts were conducted between August and December of 2013 and January to March as well as August to October of 2014 for the purposes of GPS collar deployment. Halford's, guillotine style trap box traps (76.2 cm height x 76.2 cm width x 182.9 cm length) made from a combination of steel mesh and plywood were set in areas where red foxes are observed frequently or there was a lot of evidence of fox use in the area (i.e., scat, trails, animal remains, den sites). Unfortunately it was not possible to choose trapping sites at random due to the nature of urban areas and the challenge of gaining access to large amounts of private property within the city. The outside of the traps were camouflaged with spruce boughs and other natural material and the inside was also insulated with leaves, soil and grasses from surrounding areas. The traps were baited with rabbit meat and checked twice daily. Bushnell Trophy Cam HD Max trail cameras that took 1 min video clips were set up at the trapping sites and were triggered by detecting any movement in animals via a passive infrared motion sensor. These cameras were also placed at trapping sites to gain insight into animal activity in the vicinity of the traps. If there was no sign of foxes near the trap after 7 days, then traps were moved to new locations.

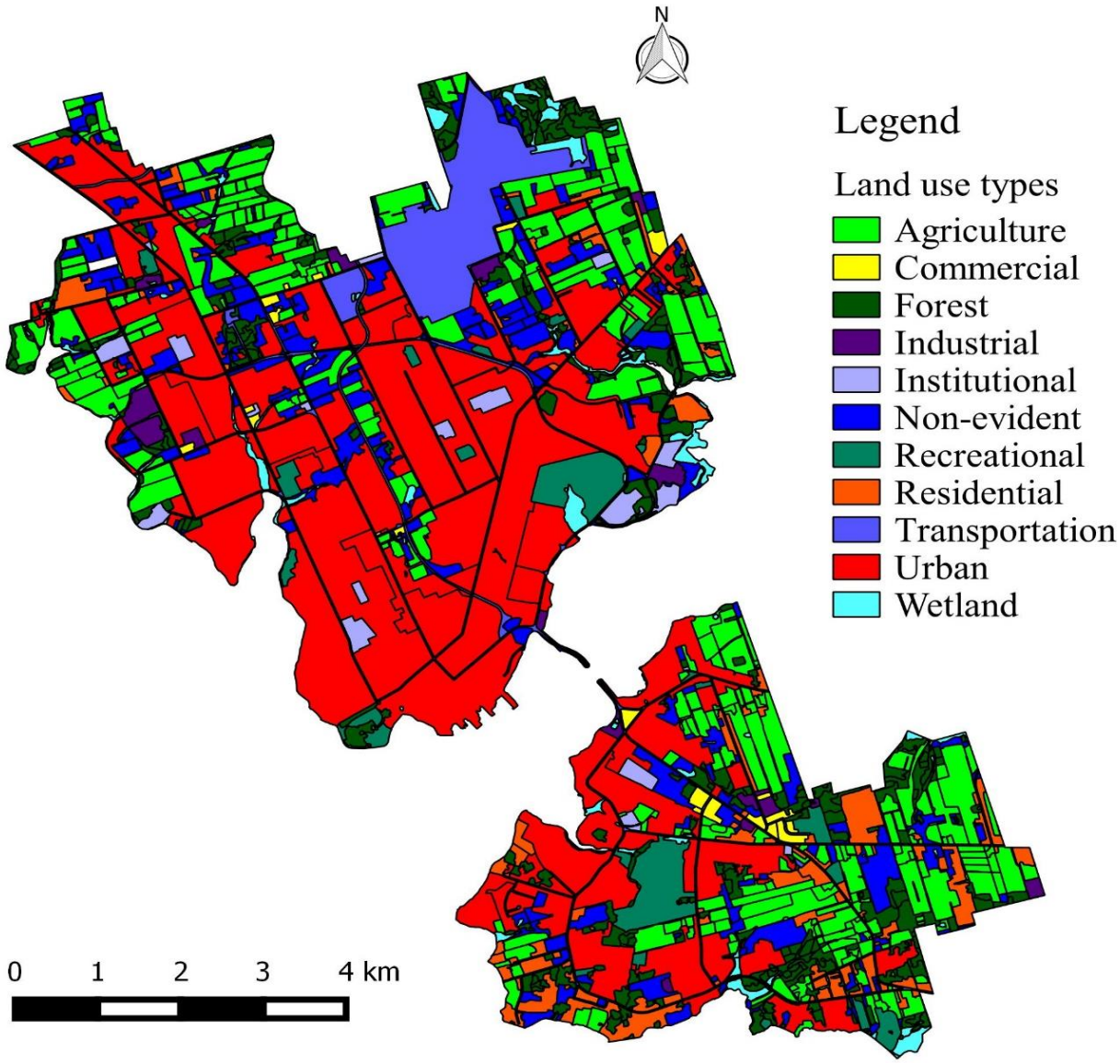

Figure 3.1. Map showing original land use classification (2010) of the study area, Charlottetown, as well as areas that were excluded from our study.

Captured foxes were anesthetized using Medetomidine (Dex Domitor; Zoetis, New York, NY, USA), 100mg/kg; intramuscular (IM) and Ketamine (Vetalar; Bioniche Animal Health, Laval Trie, QC, Canada), 100 mg/kg; (IM) and Atipamezole (Antisedan; Zoetis, New York, NY, USA), 100 mg/kg; (IM) (University of Prince Edward Island, Animal Care Protocol 13-014). A physical exam was conducted on each trapped animal to determine gender, length, weight and measure pulse and respiration rate. Vital signs were continuously monitored throughout immobilization. Age of the fox (adult or juvenile) was determined by the coloration and condition of the teeth which were examined while under sedation. Very white and sharp teeth are characteristic of young foxes whereas stained, more rounded teeth are characteristic of adult foxes (Grau et al. 1970, Gipson et al. 2000, Olifers et al. 2010)). National Band and Tag Co. steel ear tags (model # 1005-681), were attached to each ear for future identification. Four Sirtrack GPS/VHF collars with internal timed release (Model GWC171, 25mm wide, 120 g, Sirtrack, New Zealand) were used for the first portion of tracking (foxes M1, M2, F1). These collars record a GPS fix every 15 minutes with a precision error of 5-10 m for approximately 18 days. The collars are also equipped with a VHF component so that the animal can be tracked manually while wearing the collar and also to retrieve the collar after release. A Suretrak receiver by Lotek Engineering Co. (STR_1000 telemetry receiver) and standard Yagi Antennas were used to locate the collar via its VHF frequency. In addition three Lotek Wildcell SLG (230g) collars were used which also recorded a GPS fix every 15 minutes (except for one which was every 30 minutes) with a precision error of 5-10 m for a period of 14 days (foxes F2, F3, F4). A 30-minute fix schedule was tested on one fox in order to examine the battery life capabilities of the

Lotek collars, with hopes that it may be possible to get two deployments out of a single collar. This was determined to be an unrealistic expectation however, due to the condition of the collars once they were retrieved and so it was decided to revert back to 15 minutes fix schedule to obtain as much information as possible from the collars. These collars used a ground station modem and wireless carrier SIM card to upload GPS fixes every 1.5 hours.

3.3.3 Home Range Calculation and Habitat Selection

Home ranges and core-use areas of each of the collared foxes were calculated using a Home Range Analysis (adeHabitat HR) plugin within QGIS. First, the areas of 100% minimum convex polygons (MCPs) were used to define the total habitat available to foxes. MCP techniques constitute the earliest, simplest and most comparable method for calculating home ranges (Mohr 1947, Southwood 1966, Harris et al. 1990). This methodology estimates an animal's home range by connecting 100 % of the location points that make up the boundary of the range and calculating the area of the resulting polygon (White and Garrott 1990). This method is strongly influenced by outliers which is problematic because some of these boundary points may not be representative of daily movement regimes, but of isolated exploratory bouts of movement. Regardless of its downfalls, however we chose to include the MCP home range estimator as it is still frequently used when investigating home ranges across species and within species (e.g., Gompper and Gittleman 1991, Jetz et al. 2004, Nilsen and Linnell 2006) thus making this method very comparable to the literature (Nilsen et al. 2008). Furthermore, MCP methodologies have previously been reported in many studies investigating red foxes

(Trewhella at al. 1988, Harris et al. 1990, Marks and Bloomfield 2006) adding to the comparability of this method for our research.

Additionally, utilization distributions were estimated using kernel density estimators (KDEs) which give the probability of use of an area around fixed points. Utilization distributions, defined as "the two-dimensional relative frequency distribution of points of location of an animal over a period of time" (Van Winkle 1975), have been more recently applied to animal home ranges in order to describe the relative amount of time spent by the animal in any one place (Seaman and Powell 1996). KDE contours of 95% and 50% were calculated to exclude possible areas of non-use and to reveal areas of core-use, respectively. The kernel method involves a probability density function (a kernel) being placed over each data observation point in the sample. A grid is then superimposed over the data and an estimation of density is taken at every intersection of that grid. Data points that are close to a point of evaluation (a grid intersection) will contribute more to that estimate than ones that are farther away and therefore density estimates will be high in areas with many observations and low in areas with few observations (Seaman and Powell 1996).

The functional shape and width of the kernels, which determines the amount of smoothing applied to the data (known as bandwidth or *h*), (Silverman 1986, Worton 1995) was selected using an optimal smoothing method to reduce the possibility of under-smoothing (large variance), characteristic of other methods such as the least squares cross validation method (Kie 2013). The fixed kernel method was used and thus the same bandwidth value was used for the entire sampling area, whereas alternative methods such as the adaptive kernel method calculates varying bandwidths based on each

observation within the sampling area (Kernohan et al. 2001, Seaman and Powell 1996). We chose to use the fixed kernel method because it is the most widely used and produces a lower bias than adaptive kernel methods (Seaman and Powell 1996, Seaman et al. 1999).

One of the most common methodologies used to determine habitat use is to utilize animal location data (i.e., GPS coordinates) in correspondence with information on habitat type (e.g., Ryan et al 2006, Silva et al. 2009, Camps and Alldredge 2013). This technique, referred to as the "Neu" method, calculates the proportional use of habitat by examining the number of animal locations within each habitat type, assuming that animals will use habitat in proportion to its availability (Neu et al. 1974). This straight forward method applies log-likelihood ratio tests to compare the observed number of animal locations in each habitat, with the expected number of animal observations, calculating confidence intervals (Bonferroni Z-statistic) around the expected proportions to determine whether the observed proportion of usage in each habitat differed significantly from the expected.

Habitat variables for this study were determined using a modified classification scheme of PEI land use categories (Table 3.1) and included land used for agriculture, natural areas, low density human-use and high density human-use. QGIS was used to map GPS locations of collared foxes and to assign each location to a land use type. The study areas used for habitat selection analysis for each individual fox were maintained within each foxes respective home ranges. The usage of a particular land use type was defined as the ratio of GPS locations in each land use type and the total number of GPS locations recorded in the study area. Expected usage of a land use type was defined as the

ratio of area of a particular land use type divided by the total area of the study site. Habitat selection was examined for each home range calculation (MCP100%, KDE95%, KDE50%) for all individuals combined. When the foxes were categorized by sex and season, however, sample sizes were low, limiting analysis options. Therefore, in order to investigate any potential patterns associated with seasonality or gender, we combined the number of GPS locations observed for the all the foxes found in each corresponding habitat types for each season (fall, winter, summer) and for each sex (male, female) and used a log-likelihood ratio test to examine potential differences between the number of GPS locations expected versus the number of GPS locations observed in each habitat type, based on its availability. The log likelihood ratio test was then used to compare the goodness of fit of the two models (observed vs. expected) using chi-square distributions of each.

Table 3.1. Modified land use classification scheme for the purposes of this study (adapted from: the PEI Corporate Land Use Inventory (2010)) of Charlottetown where high-density human-use areas are defined as those areas used by humans every day, all year round. Low-density human-use areas are defined as areas used less by humans for specific purposes in specific seasons (i.e.: golf course) or areas that are rarely visited by humans.

Modified land use classification	Land use categories included
Agriculture	Agriculture (Experimental Farm)
High human use	Urban, residential, transportation, commercial, industrial, institutional
Low human use	Recreational, non-evident (abandoned or vacant), coastal
Natural areas	Forestry, wetlands

3.4 Results

Seven foxes were captured during this study but we were only able to obtain data from six of them (Table 3.2), as data from one collar was lost during radio tracking. Using the MCP100% method, home ranges varied between 44.4 ha and 1406.3 with a mean size of 350.2 ± 526.4 ha while the KDE95% resulted in home ranges that varied between 41.8 ha and 268.4 ha with a mean size of 119.4 ± 83.23 ha (Table 3.3). The core-use area calculated by the KDE50% resulted in home ranges from 7.3 ha to 50.1 ha with a mean size of 23.5 ± 17.3 ha (Table 3.3) and the comparison of each different contour for each fox within the urban area of Charlottetown is shown in Figure 3.2. At the MCP100% home range contour, we found the following overlaps: M1 and M2 = 227 ha, M1 and F1 = 40 ha, M2 and F1 = 37 ha, M2 and F3 = 56 ha and F2 and F4 = 87 ha. At the KDE95% and KDE50% home range contours, F2 and F4 were the only foxes with overlap at 81 ha and 10 ha, respectively.

Using the Neu method, all six foxes used all available habitat types when considering MCP100% and KDE95% home ranges. At the MCP100% contour, foxes were positively selecting for agricultural and natural areas. Similar results for agricultural and natural areas were obtained using KDE95% contours. KDE95% contours also showed that foxes utilize areas of low-human-use less than expected. When examining

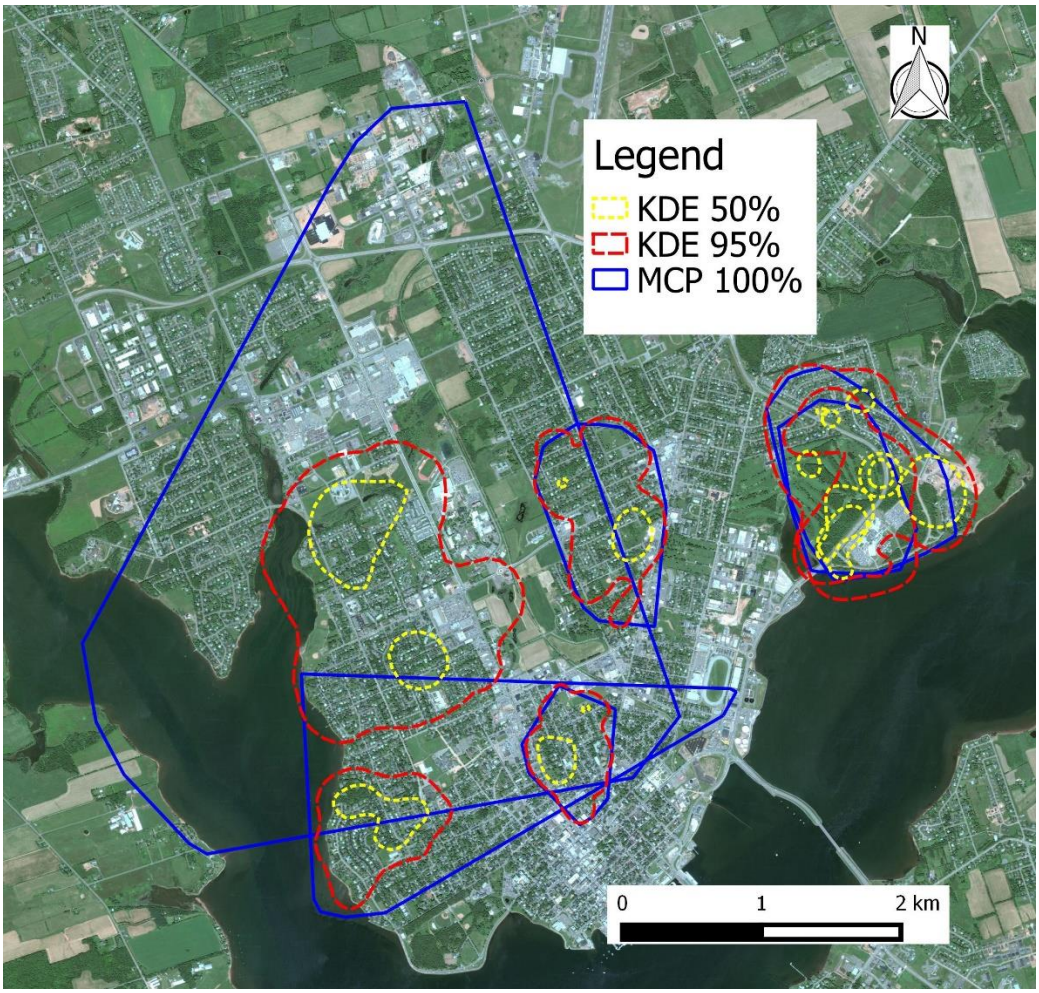

Figure 3.2. Contour map of home range boundaries for six collared foxes in Charlottetown, PEI, using minimum convex polygon (MCP) 100%, kernel density estimator (KDE) 95% and kernel density estimator (KDE) 50% home range.

Table 3.2. GPS data along with the season it was collected in for six urban red foxes captured in Charlottetown, PEI (F = female, M = male).

	F1	M1	M2	F2	F3	F4
GPS fixes collected	566	1581	1648	656	1304	1354
GPS fix schedule (minutes)	15	15	15	30	15	15
100% Minimum convex polygon (ha)	44.3	323.9	1406.3	88.0	101.5	137.3
95% kernel density estimator (ha)	41.8	64.1	268.4	95.5	86.3	160.52
50% kernel density estimator (ha)	7.3	16.3	50.1	19.8	8.4	39
Season captured	Fall	Fall	Winter	Winter	Summer	Fall

Table 3.3. Location and physical information for fox captures in Charlottetown from October 2013 – September 2015 (M = male, F = female).

Wildlife Handling Form Information for Urban Fox Captures						
Fox ID	**M1**	**F1**	**M2**	**F2**	**F3**	**F4**
Date Captured	2013-10-19	2013-10-25	2014-01-25	2014-02-24	2014-08-04	2014-09-30
Location of Capture	Inkerman Drive	Lapthorne Drive	Shell Court	Greensview Drive	Woodlawn Drive	Glenthorne Avenue
Sex	Male	Female	Male	Female	Female	Female
Age	Juvenile	Juvenile	Juvenile	Adult	Juvenile	Juvenile
Weight (kg)	6.5	6	6	6.5	5.5	5.25
Body Condition	Good	Good	Excellent	Excellent	Excellent	Excellent
Head Length (cm)	20	21	19	17	18	17
Body Length (cm)	48.5	47	50	47	45	46
Tail Length (cm)	42	38	42	39	39	36

*Overall body condition was assessed by examining the condition of fur, muscle development, fat levels, teeth, checking for any new or old injuries

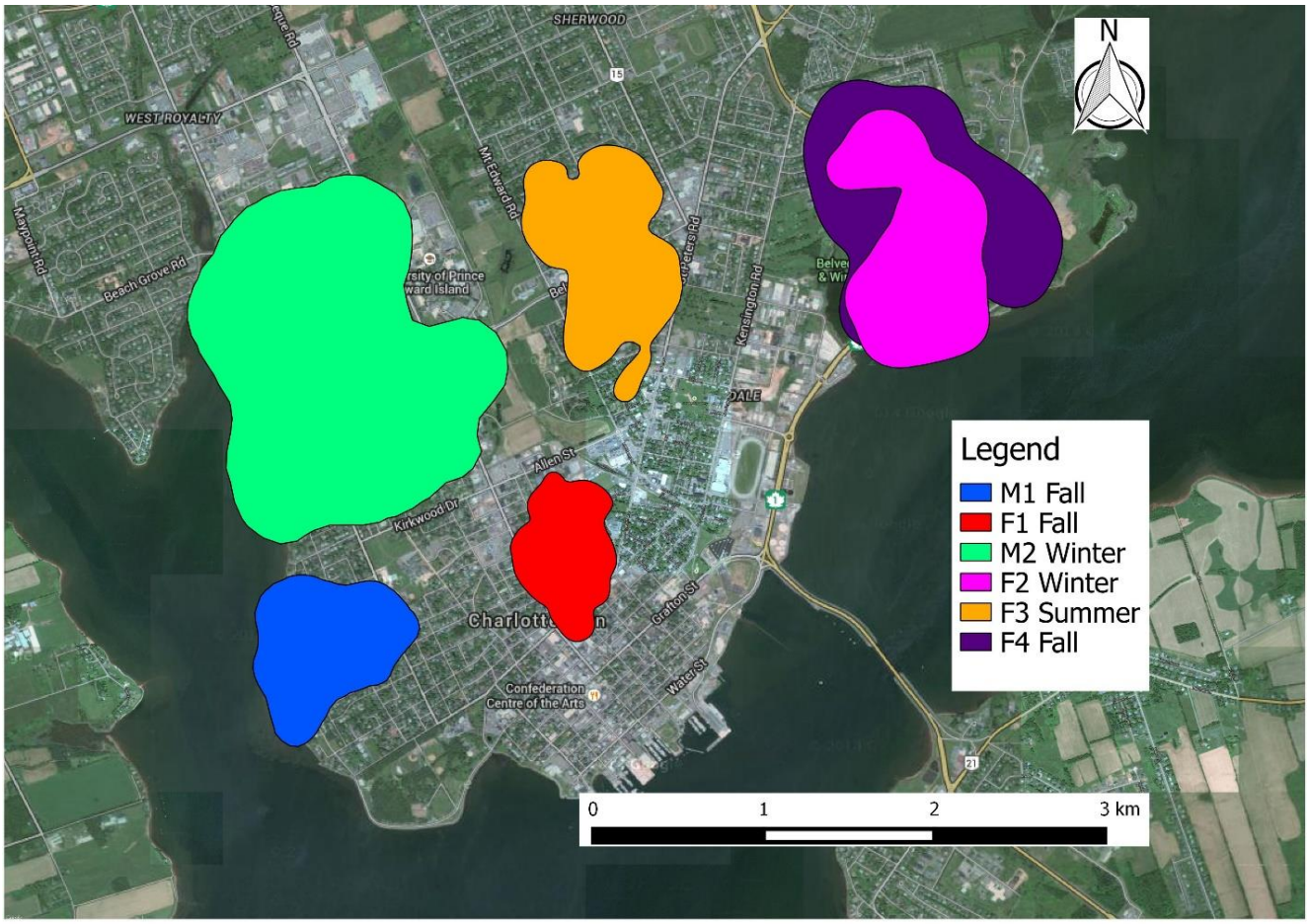

Figure 3.3. Map of Charlottetown depicting the kernel density estimator (KDE) 95% home range contour of each of the six foxes collared in this study along with the season they were captured in.

the KDE50% home range contours, agricultural areas were not used at all and low-human-use areas were used more than expected (Table 3.3)

Significant differences were detected in fall and winter when examining the number of GPS locations observed in each habitat type (agriculture, natural land, areas of low human use and areas of high human use) and the number of GPS points expected in each habitat type, based on habitat availability (fall n = 3, winter n = 2, log-likelihood ratio test, df = 3, $p < 0.05$; Table 3.5). Significant differences were also detected in both males and females when considering the expected number of GPS locations in each habitat type versus the observed number of GPS locations in each habitat type relative to habitat availability. For males differences were demonstrated at all home range levels (MCP, 95% KDE, 50% KDE) (male n = 2, log-likelihood ratio test, df = 3, $p <0.05$) and for females significant differences between observed and expected were present in both the MCP 100% and the KDE 50% home ranges (female n = 4, log-likelihood ratio test, df = 3, $p > 0.05$ (Table 3.6). These results must be interpreted with caution due to low sample sizes and the fact that several of the foxes maintaining home ranges that consisted solely of one habitat type (e.g., F2 existed solely in areas of high-human-use).

Table 3.4. Comparisons of use and availability of various habitat types within Charlottetown, PEI based on six GPS collared foxes. (MCP = minimum convex polygon, KDE = kernel density estimator)

Habitat	Observations (# GPS fixes)	Habitat Use Proportions Mean	SD	Expected use Proportion	Preference
MCP 100%					
Agriculture	13	0.0013	0.0033	0.0284	+
Natural area	653	0.1073	0.1387	0.1672	+
Low human-use area	1184	0.1768	0.1938	0.1007	-
High human-use area	5245	0.7132	0.0327	0.7036	0
KDE 95%					
Agriculture	9	0.0012	0.0024	0.0070	+
Natural area	643	0.1078	0.1408	0.1184	+
Low human-use area	1172	0.1772	0.1930	0.1603	0
High human-use area	5144	0.7137	0.3286	0.7142	0
KDE 50% (core)					
Agriculture	0	0	-	0	n/a
Natural area	452	0.1030	0.1359	0.0707	0
Low human-use area	954	0.2025	0.2370	0.2747	+
High human-use area	3275	0.6947	0.3697	0.6546	-

Comparisons were made using the Neu Method and Bonferroni confidence intervals. Preference was determined with bonferroni confidence intervals ($\alpha = 0.05$) placed on use. " + " indicates used more than expected " – " indicates used less than expected; " 0 " indicates use according to availability or non-significant difference between expected and available.

Table 3.5. The number of observed GPS points versus the number of expected GPS points based on land use availability for foxes caught in each season (fall, winter, summer) broken down by home range estimator (MCP 100%, KDE 95%, KDE 50%) Significant differences in values based on log-likelihood ratio test (df = 3, $\alpha = 0.05$)

Location of GPS Points	MCP* 100%		KDE** 95%		KDE 50% (core)	
	Observed GPS Points	Expected GPS Points	Observed GPS Points	Expected GPS Points	Observed GPS Points	Expected GPS Points
FALL						
Agriculture	0	0	0	0	0	0
Natural Areas	272	341	256	389	156	210
Low human-use	440	326	439	633	374	613
High human-use	2789	2834	2744	2417	1730	1437
P-value	< 0.05		<0.05		<0.05	
WINTER						
Agriculture	13	91	9	31	0	0
Natural Areas	381	463	387	339	296	95
Low human-use	694	248	683	387	580	496
High human-use	1202	1488	1173	1495	720	1005
P-value	< 0.05		<0.05		<0.05	
SUMMER						
Agriculture	0	2	0	0	0	0
Natural Areas	0	0	0	0	0	0
Low human-use	50	40	50	50	0	0
High human-use	1254	1262	1727	1226	825	825
P-value	> 0.05		> 0.05		> 0.05	

* MCP = minimum convex polygon, **KDE = kernel density estimator

Table 3.6. The number of observed GPS points versus the number of expected GPS points based on land use availability for each gender of fox caught (Male, Female) broken down by home range estimator (MCP100%, KDE95%, KDE50%) Significant differences in values based on log-likelihood ratio test (df = 3, $\alpha = 0.05$)

Location of GPS Points	MCP* 100%		KDE** 95%		KDE 50%	
	Observed GPS Points	Expected GPS Points	Observed GPS Points	Expected GPS Points	Observed GPS Points	Expected GPS Points
MALE						
Agriculture	13	110	9	48	0	0
Natural Areas	202	601	199	380	121	69
Low human-use	392	219	390	292	299	280
High human-use	2608	2285	2549	2427	1630	1701
P-value	< 0.05		< 0.05		< 0.05	
FEMALE						
Agriculture	0	0	0	0	0	0
Natural Areas	451	294	444	444	331	272
Low human-use	792	982	782	836	655	1045
High human-use	2637	2602	2595	2540	1645	1313
P-value	< 0.05		> 0.05		< 0.05	

Figure 3.4. Evidence of urban foxes utilizing human resources in Charlottetown as a mother fox is captured by a trail cameras taking back chunks of bread to her kits at an urban den site (2014).

Figure 3.5. Evidence of urban foxes utilizing human resources in Charlottetown as this young kit sits beside a fully cooked chicken captured by a trail camera at an urban den site (2013)

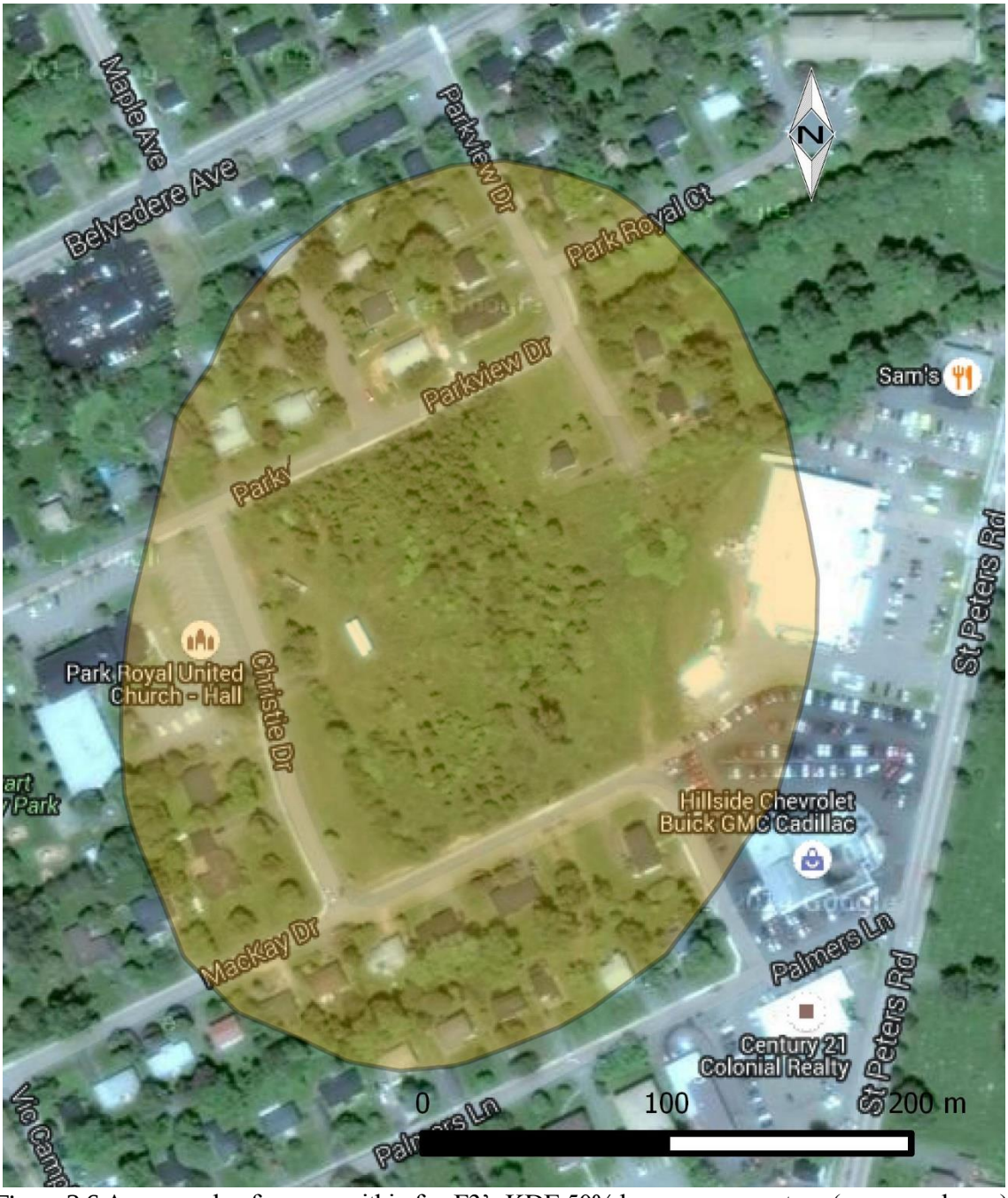

Figure 3.6 An example of an area within fox F3's KDE 50% home range contour (orange polygon) which demonstrates characteristics of a "natural" area within an area of high human use.

3.5 Discussion

Red foxes are typically considered habitat generalists, and their ability to adapt to lower-grade habitats has contributed to their success within urban areas worldwide (Gloor et al. 2001, Scott et al. 2014). This, however, does not imply that they do not exhibit preferences for certain types of habitat. In this study we found that foxes within Charlottetown selected for natural land and areas of low human use despite gender and the season in which they were collared. Historically, the home ranges of urban red foxes have been found to be smaller than those of foxes living in rural areas (Sálek et al. 2014, Iossa et al 2010, Bateman and Fleming 2012) and thus we expected the foxes of Charlottetown to follow similar patterns. We found, however, that urban fox home range sizes in PEI appear to be larger than many reported in other urban areas worldwide, and seasonally, are in fact comparable to red foxes living in rural areas of PEI (Silva et al. 2009). The average MCP home-range values obtained in this study are quite large (mean of 350.2 ha). Other studies demonstrate urban fox home range size to be approximately: 20 ha (Bristol, United Kingdom, Harris and Baker 2001), 45 ha (Melbourne, Australia, White et al.2006) and 52 ha (Toronto, Canada, Adkins and Stott 1998). Several factors may explain these differences, including: city size and geography, human population size, degree of habitat fragmentation, and fox population densities. With regards to such factors, Charlottetown is a small city, with low human density. Other cities where foxes have been studied include, Toronto which has an area of 630 km^2 and a human population of over six million (Statistics Canada 2014) while Bristol, UK, has an area of

110 km^2 and a human population of 442,500 (Bristol City Council 2014). With the 44.3 km^2 of Charlottetown's urban area (PEI Department of Environment, Energy & Forestry 2010) along with the human population reaching only 34, 560 (PEI Statistics Bureau 2014), it is merely a fraction of the size of other cities containing substantial urban fox populations and thus is may be more realistically compared to a town or suburban area. In fact, rural home range sizes of foxes on PEI have been reported to be between 105.7 – 168.8 ha at the MCP100% level (Silva et al. 2009). Although this may appear to be quite a bit smaller than what we have found in Charlottetown, it is important to consider the time of year in which measurements were taken. Data for rural foxes were collected between April and September, while data for foxes in Charlottetown were collected from August until March. During the summer months ranges are likely smaller in both rural and urban populations due to intense kit-rearing and denning behaviours, whereas, fall and winter months may be key periods for juvenile dispersal, exploratory behaviours and mate selection and thus explain the larger ranges of male foxes during this time in urban areas (See Table 3.2). Although for this study one fox was captured in the summer, this individual was a juvenile and thus her home range size is not resultant of reproductive behaviours such as kit-rearing, but likely of the gradual range expansion that may occur prior to fall dispersal.

It is also likely that the level of habitat fragmentation within other larger cities that maintain urban fox populations (e.g., Bristol, London, and Toronto) are quite different from that of Charlottetown. Although habitat fragmentation information for

Charlottetown was not available, nor was it the focal point of this study, we assume that with less busy roads, fewer residents and the lack of large buildings, habitat patches would be larger and more frequent. This would allow foxes to move through the entire urban area with relative ease, and therefore promote the use of larger home ranges.

Other possible reasons for fox home range size variations within urban systems may be the distribution of resources throughout the city. Carnivores in particular are known to alter movement and spatial patterns based on food abundance and distribution (Jepsen et al. 2002, Messier 1985, Patterson and Messier 2001, Prange et al. 2004). For instance, resources provided directly or indirectly by humans are generally concentrated into superrich patches in large cities (Prange et al. 2004). Therefore it is not surprising that foxes within Bristol for example, maintain smaller, more stable home ranges. In comparison, Charlottetown, being a smaller, and much less populated urban area, contains resources that are likely much more spread out, promoting larger home range sizes. In addition to the size of the city, differences may exist between fox home ranges in Charlottetown compared to other areas of the world due to the data collection period we used as well as local climate and the associated challenges. For example, Atlantic coastal climate patterns, likely lead to the accumulation of more snow on PEI, than in cities such as Toronto or Bristol which could lead to larger winter home range sizes during the winter. Most likely, however, is the possibility that the home range sizes of foxes in this study simply represent the opportunistic nature of foxes to adapt to a specific urban setting, in this case, Charlottetown.

Although little is known about the dispersal behaviours of urban red foxes on PEI, our data indicates that only male foxes (M1 and M2) demonstrated exploratory movement bouts that may qualify as the initial phases of dispersal, as indicated by the MCP home range. Juvenile foxes have been known to start dispersal between September and December at approximately six to eight months of age (Lloyd 1980). Movement bouts such as these occur largely when juveniles leave their natal range in search of a vacant territory where they can invest in future breeding opportunities for themselves (Soulsbury et al. 2011). Furthermore, juvenile males are more likely to disperse at this time as a result of competitive behaviour characteristically demonstrated by the dominant male fox within the home range. This behaviour usually begins in the fall and continues until the juvenile vacates the natal territory and is thus no longer a competitor during the upcoming breeding season (December and January) (Henry 1986). Fox M1 exhibited several of these exploratory movement bouts after which he returned to the area of normal daily activity. This type of behaviour is common in dispersing juvenile foxes, however, as they may take off one day, never to return to their natal range, or they may conduct several shorter, exploratory bouts, (such as those demonstrated by M1) initially before determining which direction to set off in permanently (Soulsbury et al. 2010).

Another factor that may explain the outliers in MCP100% home ranges is foraging excursions. This may explain the isolated moves demonstrated by M2 (juvenile male in winter) who was collared from January 26th 2014 – February 13th, 2014, a period in which 33.8 cm of snow fell and where the snow on the ground ranged from 24-39 cm

in depth (Environment Canada, Historical Climate Data). Winter snow accumulation is known to be an important determinant in carnivore home range size as it can drastically reduce the primary productivity of an area and consequently reduce prey density (Jedrzejewski et al. 2007, Mattisson et al. 2013). Although red foxes are diet generalists, snow accumulation is likely to make foraging for food items substantially more difficult and may require foxes to travel further distances to obtain sufficient energy sources. Support for this explanation is provided by Tsukada (1997) whose study demonstrated that concentrated food distributions within Shiretoko National Park (Japan) have led to unique foraging ranges of foxes that include seasonally available food outside of their normal territories.

It is not surprising that males in this study participated in more exploratory movement bouts and maintained larger home ranges as several studies have found that gender significantly affects home range size (Wilson 1975, Cook et al. 1976, Eisenberg 1981, Gehrt and Fritzell 1997). Females generally adopt smaller home ranges as their spatial patterns are focused on the distribution of resources in order to ensure adequate nourishment for themselves and their young. Males are known to occupy larger ranges which, in many cases, the size is determinant upon the distribution of females in the area for mating purposes (Rowell 1988, Cluttonbrock, 1989, Gehrt and Fritzell 1997). The lack of exploratory movement bouts demonstrated by female foxes in this study may be explained by are several possible reasons. First, it is common within red fox social groups that juvenile females will not disperse within the first year of their life. Instead, they are

allowed to remain within the natal range as a subordinate female in order to help provide provisional care to the cubs of the dominant female (Macdonald 1979, Zabel and Taggart 1989, Baker et al. 1998). Ultimately, this behaviour increases the survival rates of the cubs and therefore providing the group with indirect fitness benefits (von Schantz 1984, Zabel and Taggart 1989, Baker et al. 1998). Secondly, the smaller female home ranges at both the MCP100% and KDE95% level could be indicative of corresponding natural resource distributions. Multiple areas of high resource abundance within the home range may eliminate the need for exploratory foraging excursions.

The notion of home ranges corresponding to the distribution of natural resources is also supported by our habitat selection analysis. Foxes, like other organisms will choose to spend their time in some habitats over others based on the resources that exist there. At both the MCP100% and KDE95% home range levels, foxes in Charlottetown demonstrated preference for agricultural land and natural areas. These areas may offer habitat types that support a wider abundance of prey species for the red fox, explaining why they spend more time here. For example, the natural area of Hermitage Creek, in the north-west corner of Charlottetown, consists of a salt water marsh, a fresh water stream and duck pond, stands of large trees and an open grassland. Wooded areas are ideal habitats for a variety of avian, rodent species. A recent study in Charlottetown has also found that foxes have been known to take advantage of various aquatic species such as frogs, fish and snails (Robbins 2014, unpublished data) which are likely found in the stream-fed pond of this region. This natural area is an important part of fox M2's

KDE95% and KDE50% home ranges, and although this area is not very large, it is used heavily by this individual. Furthermore, an active den site was located in this area with several foxes being observed frequently during den surveys. The preference for agricultural areas may also reflect prey abundance as they are known to house large populations of several rodent species (Silva et al. 2000) as well as features such as hedge rows bordering fields, which may offer optimal resting sites.

In addition to the availability of natural resources, anthropogenic resources may also play a role in home range size. A recent survey conducted in Charlottetown reported that 32% of respondents (n = 286) have participated in feeding foxes in the past or would be willing to feed the foxes in the future (Martin 2015). This suggests that handouts provided by city residents may be a valuable resource for urban foxes within Charlottetown. Images captured by trail cameras placed at den sites also support this as human food items such as full cooked chickens and bread have been documented at den sites (Figures 4.6 and 4.7). Thus, we suspect that foxes living in areas of high human density have access to a greater abundance of anthropogenic resources due to the likelihood of a higher density of people resulting in a higher density of "fox-feeders". Our findings support this idea as Fox F1 has the smallest home range at both the MCP100% and KDE95% level (44.3 and 41.8 ha respectively) while living in a densely populated downtown neighborhood with minimal natural green spaces. Although survey and anecdotal evidence support this hypothesis, previous research directed towards the diet analysis of both urban and rural red foxes in PEI did not detect large quantities of

anthropogenic resources within stomach content samples (Bullerwell 2014). These results could imply that foxes do not rely solely on anthropogenic resources, despite exploiting them when they are easily obtained. Otherwise, it may be reflective of samples collected outside of areas of high-human density.

When considering seasonal behaviours of the foxes at the home range level (KDE95%), the three foxes that were collared in the fall (M1, F1 and F4), were observed less frequently than expected in natural areas and areas of low human-use and more often than expected in high human-use. This may suggest that the importance of anthropogenic food varies with season and that the opportunistic nature of foxes allows them to shift their behaviours and movements based on such variation. For instance, it is possible that in the fall, when juveniles begin to fend for themselves, along with the development of colder weather and less abundant natural resources, urban foxes may choose to exploit anthropogenic resources more frequently. This could explain why the home ranges of these three individuals are located mainly in areas of high human-use. These results must be interpreted with caution, however as is it possible that the low sample size (n=3) has created a potential bias, as two of three of these foxes, (M1 and F1) exist in areas where natural green spaces and areas of low human-use are not present.

When considering smaller spatial scales within home ranges, core-use areas contain essential resources for the animal such as shelter, diurnal resting sites, den sites and food sources, therefore these are the areas in which the animal spends most of its time. For this reason, core-use areas are particularly important for conservation and

management agendas. Sizes of the core-use (KDE50%) areas of Charlottetown's foxes ranged from 7.3 ha (F1) to 50.1 ha (M2) with an average size of 23.5 ha. In comparison to a home range study conducted on rural foxes of PEI, where core-use size averaged only 10.4 ha (Silva et al. 2009) urban foxes seem to maintain larger core-use areas. As previously mentioned these dissimilarities may be attributed to the season in which the data were collected and corresponding life history traits. For example, the core-use areas of rural foxes were measured during denning and kit-rearing and when movements may be much more concentrated as foxes care for vulnerable young. Whereas, core-use areas for urban foxes in this study were measured in every season except the spring when kit-rearing occurs for foxes. In fact, it is likely that with the urban foxes, other significant reproductive behaviours such as dispersal and mate selection impacted the size of core-use areas. In addition to reproductive behaviours, larger core-use areas in urban landscapes may be contributed to a more spread-out distribution of food and shelter resources due to the increased habitat fragmentation of the urban landscape.

Foxes in Charlottetown demonstrated a preference for regions of low human use within their core areas (KDE50%). For the purposes of this study, areas of low human use include recreational land such as golf courses and sports fields as well as abandoned/vacant land and coastal habitat. Similar to other studies on urban foxes, our data may indicate that, while food availability plays a role in the selection of core-use areas, diurnal shelters, den sites and resting sites may be the most important determinant of core-use habitat selection. Supporting evidence is provided by a recent study

conducted in Charlottetown which located 49 fox dens in areas of low human-use (Lambe 2014, unpublished data). Likewise, a study conducted in Toronto located 20 urban fox dens, most of which were found on golf courses (Adkins and Stott 1998) and a study in Melbourne reported that areas of low-human disturbance were selected based upon the presence of certain resources such as thick vegetative cover which allowed for secure day-time rest sites (Robertson et al. 2000, White et al. 2006, Marks and Bloomfield 2006).

In addition to providing abundant natural spaces for foxes to utilize for den and rest sites, urban golf courses may also provide foxes with predictable seasonal resources in the form of food handouts from golfers. It has been found that generalist carnivores (i.e., raccoons, opossums, foxes), capable of utilizing both anthropogenic and natural resources are more likely to maintain home ranges in urban and suburban areas based upon the predictability and abundance of concentrated anthropogenic resources (Schinner and Cauly 1974, Hoffman and Gottschang 1977, Rosatte et al. 1991, Prange et al. 2004, Bozek et al. 2007). Thus, it is plausible to assume that seasonal shifts in such resources could be reflected in core-use areas of urban wildlife. Anecdotal evidence from employees of urban golf courses in Charlottetown report that foxes are known to follow the beverage cart at close range for several holes, knowing that they are likely to be fed by the next group of golfers (Staff of Belvedere and Fox Meadow golf courses, personal communication 2014). Our findings clearly demonstrate the adaptability of foxes to select for habitat based on the availability of seasonal resources. For example, two foxes in this

study (F2 and F4), both maintained home ranges within the same urban golf course, yet demonstrated some differences in respective core-use areas. These inconsistencies may have existed based on the fact that fox F4 was collared in the fall and thus was likely able to exploit human resources during this time as the course was still heavily used by golfers. Whereas fox F2, collared during the winter, demonstrated core-use areas more indicative of resources naturally occurring on the golf course, such as optimal denning sites, as human activity, and consequently human provided food, is limited on the golf course during this time.

With this study we were able to look at the core-use area of both males and female foxes in Charlottetown. Similarities in habitat selection exist in the preference for areas of high human use at the KDE95% level while at the KDE50% level, females were found more than expected in areas of high-human use and natural areas in contrast to males selecting more natural areas. The selection of areas of high-human-use by the foxes in this study could reflect potential resources found there, such as food provided by humans, as well as pockets of relatively undisturbed land, like in the case of fox F3 discussed previously, that may exist here despite high human densities. In order to fully understand differences that may exist between the selection patterns of male and female foxes in Charlottetown it would be necessary to collect data on more individuals of each sex.

For a more comprehensive understanding of core-use areas within urban landscapes, it may be important to consider identifying habitat types at a fine spatial

scale. In this study, seasonal investigations into the core-use areas of the foxes have indicated that in the summer (fox F3) used areas of high-human-use more than expected. Although this accurately represents the habitat types used for this study, further investigation into the core-use area of F3 (via GIS and ground surveys) have determined that pockets of natural areas important for urban wildlife may exist within the urban matrix at a smaller spatial scale. This is demonstrated in Figure 3.6, where the core-use area of F3 contains multiple fox den sites (Lambe 2014, unpublished data) grassy expanses, wooded stands and a small stream, yet is considered an area of high human-use by corporate land use files.

When considering urban wildlife, areas of core-use are of the utmost importance for wildlife management officials as these are the areas within the urban matrix which the animal chooses to spend the majority of its time. Understanding why foxes select these areas and what essential resources exist here may help in the development of strategic management plans designed to encourage healthy fox-human relationships. By protecting such areas, in combination with developing small patches of "natural" land within urban areas it may be possible to limit the conflict between humans and foxes that may arise by foxes utilizing residential backyards for intensive periods of denning or foraging

It is important to note that depending upon what spatial scale is being considered, habitat selection preferences may change. For instance, while foxes in this study selected for natural and agricultural areas at the larger home range scale (MCP100%, KDE95%), they selected for only low-density human use at the core-use scale (KDE50%). In fact,

agriculture was not even present in any of the fox's core-use areas. Not selecting for agricultural areas at a small spatial scale may be a reflection of the small amounts, if any, of agricultural lands existing within the individual home ranges, but, based on the time of year the data was collected for each fox, could also reflect shifts in seasonal vegetation and crop growth. For instance, foxes were observed at a den site which was located in a crop field of the Experimental Farm. This den has persisted for two years and is heavily used between March and June during the kit-rearing season. In both years the foxes have moved on before the end of June, when cultivation of this field began (Lambe 2014, unpublished data). When the field is not being used for crops it offers the foxes a semi-natural area with low human disturbance and plenty of surrounding resources.

In addition to size, examining home range overlap may provide insight into: the degree of territoriality being expressed by individuals, regions of high food abundance, and information about genetic relatedness (McLoughlin et al. 2000). It has been suggested that with mammalian carnivores, in areas of high food abundance, home range size may decrease as not much space is needed to obtain sufficient resources (Šálek et al 2015). These resource rich areas are also known to promote a higher degree of home range overlap, and diminished territorial behaviours as intruder pressure increases to exploit such resources (Myers et al. 1981, Wolff 1993, McLoughlin et al. 2000, Šálek et al. 2015). It is also possible that observed patterns of home range overlap are indicative of genetic relatedness as the allowance of family members within an individual's home range acts as a mechanism to indirectly increase the fitness of that individual by the

increasing the survival likelihood of kin (McLoughlin et al. 2000). It is believed this is the case for the two foxes in Charlottetown (F2 and F4) that demonstrated substantial home range overlap within this study. Based on the age, gender and time of year at which both foxes were observed, it is likely that F4 is the offspring of F2 and was permitted to stay within the natal range to become a helper to the dominant female in terms of raising future litters (Baker and Harris 2004, von Schantz 1982). Although the home range of the adult female appears to be smaller than that of the juvenile, this is likely due to the time of year when data was collected. The adult fox (F2) was collared in late February and thus the smaller size of her home range may have been due to concentrated den preparation regimes, as it is likely she was getting ready to give birth.

Overall, we have found that the average home range size of foxes in Charlottetown is quite large in comparison to foxes existing in other urban areas around the world, and these sizes are in fact more comparable to the home range sizes of rural foxes. These larger sizes may be resultant of the seasons in which the data were collected and the reproductive behaviours (i.e., dispersal, mating, searching for den sites) associated with each time period. Additionally the large size of fox home ranges in Charlottetown may be attributed to the distribution of resources (i.e., den sites, food, and resting sites) within the city based on factors such as human population density, the distribution of natural areas and the level of habitat fragmentation that exists within Charlottetown. Foxes in this study showed habitat preference for natural areas and areas of low human-use, indicating that minimally disturbed areas within the urban matrix may

be ideal for denning and rest sites. Furthermore, seasonal shifts of core-use areas may suggest variation in resource abundance, both natural and anthropogenic, thus providing further evidence of the adaptable and opportunistic nature of the red fox.

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Chapter 4

Spatial and temporal movement patterns of urban red foxes on Prince Edward Island, Canada

4.1 Abstract

Studying the movement patterns of animals can allow us to gain insight into many aspects of their ecology such as home range patterns, foraging strategies, patch-use, and diet. Although the literature surrounding animal movement and theoretical movement models is extensive, there exists a lack of studies conducted within urban landscapes. With ever-expanding global urban development, as well as the increased abundance of adapted wildlife species into these areas, it is important to understand how carnivores such as red foxes are foraging, what areas of urban landscapes they are using and how the confinement effects associated with such highly fragmented landscapes affect these movements. This knowledge is important for conservation and management strategies, as well as the health and well-being of both the humans and wildlife residing within urban areas. The goals of this study specifically were to spatially and temporally investigate the effects of confinement on the movement patterns and foraging strategies of urban red foxes, in Charlottetown, PEI as well as to determine if seasonal and gender based differences exist. Using a correlated random walk as our null hypothesis, we investigated the movement features of six foxes over three seasons (fall, winter, summer). These

features included: net-squared displacements, turning angle and move-length distributions and fractal patterns. In addition we investigated the emergence of clusters through GPS data as a way to detect patch use and the mechanisms driving patch use. Our results indicate that, despite the patchiness of urban environments such as Charlottetown, foxes are not demonstrating the directional persistence associated with correlated random walks, but more Brownian (random-like) characteristics. This could be due to an abundance of resources, both natural and anthropogenic. Furthermore, movement patterns reveal different features in winter than in fall likely based on resource availability and the difficulties of foraging associated with snow cover. It is important to keep in mind that although directed movement, characteristic of correlated random walks, was not detected in this study, it is possible that this could be resultant of confinement effects and physical structures associated with urban landscapes and thus the detection of habitat patches across all spatial scales may be useful for future studies.

4.2 Introduction

Studying the patterns associated with animal movement can help us understand how animals perceive and utilize their environments and what strategies they use to obtain the resources necessary for survival (e.g., Kareiva and Shigesada 1983, Crist et al. 1992, Etzenhouser et al. 1998, Ball et al. 2000). As urban areas continue to expand, negative confrontation between humans and wildlife becomes more probable. One of the main concerns for wildlife, surrounding human development and the encroachment of wild lands, is the detrimental effects of habitat fragmentation. Habitat fragmentation, as

defined by Lord and Norton (1990), is the breaking up of a large intact area of vegetation into smaller units. Natural habitats are becoming increasingly fragmented as human populations grow and anthropogenic development continues globally. These alterations to the environment can be directly responsible for shifts in complex ecological systems within these landscapes. As a result, the confinement and degradation of habitat can lead to a patchy distribution of resources, incurred risk to animals travelling between these patches and increased competition among foragers. Localized changes such as these have been known to influence the movement patterns of animals within these fragmented landscapes (Johnson et al. 1992, Turchin 1998). Examples of these negative interactions include increased bold behavior of wildlife due to human-feeding, potential attacks to humans and domestic pets as well as the transmission of diseases to humans and pets. It is important to understand how human development is affecting these movement patterns. If we understand dispersal patterns of wildlife, spatial heterogeneity of the landscape and the distributions of the species, there exists a much greater chance of implementing successful conservation and management strategies. For example, many epidemiological studies rely on animal movement information in order to predict and monitor the propagation of serious zoonotic diseases such as rabies within human-populated areas. The motivation for most animal movement is the necessity to acquire resources. The search strategies used to obtain these resources are simply decision-making processes that result in a series of displacements and orientations.

Turchin (1998) describes a ‘move’ made by an animal to be the displacement between two consecutive stopping points. Whereas a ‘path’ is the complete spatio-temporal record of all of the moves made by an animal during a particular observation period. A ‘step’ is another common term used in movement analysis and it is defined as the displacement between two successive coordinate fixes. Some common measurements used to characterize movement paths include: total length of the path, net displacement, which is the straight line distance from the beginning to the end point of a path, tortuosity, which measures the twistiness of the path and absolute direction (Turchin 1998). As the habitats in a landscape change, so should these measurements of movement.

The optimal foraging theory (OFT), developed by MacArthur and Pianka (1966) describes how foraging organisms will employ specific search strategies in order to maximize energy intake while limiting energy expenditure (Pyke 1984). This elucidates why animals will utilize different search strategies and movement patterns based on different habitats. For example, if an animal encounters a resource-rich patch, certain mechanisms of the movement path of this animal will be altered in order to increase search efficiency. These mechanisms include increased looping and spiraling, increased turning frequency, decreased move length, and recognizing the patch edge by turning back when profitability decreases below a critical threshold level (Marrell et al. 2002, Bell 1991, Mueller and Fagan 2008, Salvador et al. 2014).

In order to study movement, field methods such as GPS and radio tracking are commonly used to obtain animal movement data. Theoretical models allow us to gain an understanding about the underlying mechanisms driving animal movement. When we obtain a movement path from a particular animal we get a "snapshot" of what the movement looked like, but don't know "why" it looks like that. Furthermore, by identifying a particular movement path, or paths, with a given theoretical model, we are able to categorize patterns (e.g., random walks, Lévy Walks, etc.). The ability to generalize in this way allows us to understand the movement patterns and make predictions. This is essential information for wildlife and land management experts and related stakeholders.

Although theoretical models cannot describe entire systems, they are intended to explore particular hypotheses and predict how the model will change with different model parameters (Turchin 1998). Computer simulations are also useful tools to study movement, as they can be used for testing basic assumptions in animal movement models. These computer simulations are particularly valuable when field data are limited; research questions require specific conditions to be modeled or when certain theoretical models do not represent the complexity of natural landscapes (Jenkins 2010).

The two main categories of theoretical models pertaining to animal movement are Eulerian models and Langrangian models. Eulerian models are implemented at the population level and focus on a point in space which can be characterized by the densities or fluxes of moving organisms and incorporate such parameters as dispersal and

avoidance rates. One of the most basic and well established Eulerian models that has been developed for ecological purposes is the Lotka-Volterra Model (Lotka 1925). This model uses non-linear differential equations to describe the populations of predators and prey and how they interact through time.

$$\frac{dx}{dt} = \alpha x - \beta xy \qquad (4.1)$$

$$\frac{dy}{dt} = \delta xy - \gamma y \qquad (4.2)$$

Where: x = the number of prey

y = the number of some predator

$\frac{dx}{dt}$ and $\frac{dy}{dt}$ represent the growth rates of two populations over time

t = time

α, β, δ,and γ = positive real parameters describing the interaction of the two species.

Langrangian models, conversely, focus on the movement patterns of individuals and consider factors such as direction, velocity and acceleration. It is imperative to remember, when using these models, that animal behaviour, specifically animal movement is not a regular or continuous event and differs between individuals (Kramer and McLaughlin 2001). Examples of Langrangian models include the Brownian random walks, correlated random walks and Lévy flights. These models will be discussed in further detail below.

The simplest of the theoretical models used to describe animal movement is a Brownian random walk (BRW), or diffusion model. In this model, movement paths are

composed of a series of random steps where the animal (walker) is equally as likely to move in any direction with no persistence or bias (Turchin 1998). The simplicity of this model, however, does not take into account the natural behaviours of most animals and therefore its applications in animal movement analysis are limited. Some studies that have been successful in identifying Brownian like movements generally involve organisms with poorly developed sensory systems such as many insect herbivores (Kareiva 1985). However, random Brownian movements can also apply to animals with highly developed sensory systems, such as homing bird species when no directional cues are available to them due to the distance to their target (Griffin and Hock 1949).

The correlated random walk model (CRW) describes movement bouts similar to Brownian movement, except there is directional persistence present (Turchin 1998). Directional persistence means that there exists a restriction of the turning angle to a limited range (e.g. -30° and +30°), preventing the walker from returning to its previous location immediately, therefore allowing the animal to proceed in a particular direction. Thus there also exists a correlation between the directions of consecutive steps. CRW models have been successfully applied to animals ranging in body size from insects (eg: Kareiva and Shigesada, 1983), to large mammals (Bergman et al. 2000, Märell et al. 2002), modeling movement patterns over both small and large temporal and spatial scales (Young & Shivik, 2006). Animal movement reflecting correlated random walks have been recognized in species such as; cabbage butterflies (Root and Kareiva 1984), reindeer (Märell et al. 2002), and caribou (Bergman et al. 2000).

Lévy walks are another type of movement model, characterized by a power-law distribution of the move lengths demonstrating scale-invariant behaviour (Shlesinger et al. 1993, Marell et al. 2002, Ramos-Fernandez et al. 2004). The underlying mechanisms of such movement gives rise to two distinct searching states. While in a resource-rich patch, foragers will optimize their search strategies by making smaller moves with a broad range of turning angles. Once the resources of such patches have been depleted, the forager will switch to a search strategy characterized by longer and straighter moves, in an effort to increase the likelihood of encountering novel resource patches (Humphries et al. 2012, Viswanathan et al. 2011, Bartumeus and Catalan 2009, Viswanathan et al. 1999, Benhamou 2007). For Lévy walks, the power-law distribution generally adopts this form:

$$N(x) \sim x^{-a} \qquad (4.3)$$

x = move length

a = power-law exponent

Although this distribution is peaked for small move lengths, the long tail of the distribution implies that longer move lengths will also be observed, but at lower frequencies. This implies that Lévy walkers may demonstrate some step sizes of longer length, resulting in a faster growing mean squared displacement, in time, than that of random walker with constant step lengths or a normal distribution of step lengths (Ramos-Fernandez et al. 2004). Another way to determine if the movement pattern is Lévy like is to examine the tail portion of the move-length distribution (see equation 4.3).

Many successful Lévy search models indicate that the optimal power-law exponent occurs for $a \simeq 2$ (Ramos-Fernandez et al 2004, Viswanathan et al. 1999, Viswanathan et al. 1996). This power-law move-length frequency distribution has proven to be successful in describing the movement of many species in the context of optimal foraging theory, including: jackals (*Canis adustus;* Atkinson et al. 2002), wandering albatrosses (*Diomedea exulans*; Viswanathan et al. 1996) and spider monkeys (*Ateles geoffroyi;* Ramos-Fernández et al. 2003).

A variation in the correlated random walk model, the composite correlated random walk (CCRW), emulates a Lévy-like movement by incorporating a similar "two-state" foraging mechanism. For example, in a resource-rich environment turning angles will be large and a small step size will be exhibited by the animal as it successfully forages. In a resource-poor environment, however, in which a searching animal wants to move through quickly in order to reach outlying areas of good quality, movement patterns will demonstrate narrow turning angles and larger step size. They differ, in that switching modes in a CCRW model is triggered externally by the presence or absence of resources, whereas in a true Lévy walk, the trigger is internal and the animal is actively using a multi-scale movement pattern to search for resources, even when not encountering any food (Benhamou 2007, Reynolds 2013).

Another well-established two-state foraging model is the area intensive searching (AIS) strategy. In this model, the forager changes between two salutatory states: 1) fast motion and degraded perception which is intended to help the animal reach distant

foraging patches when resources are low in their current area and 2) low net-displacement and high tortuosity which allow the animal to focus on prey detection in a resource-rich patch. This search strategy is different from previous examples as the decision to change states is not based merely on the quality of the habitat and the resources that exist there, but also according to a time frame that the forager should remain in a given state so not to waste energetic stores. This strategy, therefore, generally leads to greater efficiency than random search approaches and has been observed in species such as free-ranging Bison in Alberta (Fortin 2003) as well as African antelope (Underwood 1982).

When attempting to determine movement patterns in animals it is important to be aware of the particular processes that give rise to these patterns. Benhamou (2007), conducted important work in the field of animal movement patterns, where he demonstrated that it is possible to generate a Lévy-like walk (LW) using the criteria required for a composite correlated random walk (CCRW). For example, CCRWs are able to mimic the characteristics of a LW when mixtures of random walks are being used in area-concentrated phases of searching within patches, in combination with search phases representative of the large distance traversing phases between patches. In this circumstance it may appear that the LW movement pattern exhibits a more efficient search strategy, but in reality this process may not be generated by a true LW process (in which the distribution of step lengths obeys an inverse power law with an exponent $a <$ 3). It must also be ascertained that the pattern observed is not solely generated by the way

the animal interacts with the environment through some classical movement processes (i.e., CCRW) (Cole 1995, Boyer et al. 2006, Benhamou 2007).

In addition to using theoretical movement models, another way of gaining insight into how animals perceive and react to the fragmentation of their environment is by using fractal analysis. Fractal analysis is a powerful tool that has been used in animal studies to measure the "tortuousity" of a particular movement path as a way to determine how an animal uses habitats at different spatial scales (Milne 1991, Benhamou 2004, Doerr and Doerr 2004, Roshier et al. 2008, Ehlers et al. 2014). For example, in a resource-rich patch, the movement of the forager will likely be more compact, random and characterized by short move lengths and a range of turning angles. Such a path would be classified as tortuous. In contrast, for more directed or biased movement in a particular direction, the path will be straighter with turning angles tightly centered around zero degrees. The fractal dimension (D) for movement paths lies between 1, when the path is less tortuous, and 2, when a path is so tortuous that it becomes plane-filling (Turchin 1996, Nams & Bourgeois, 2004). The following equation can be used to estimate the fractal dimension by forming a theoretical relationship between the length scale of the path and the total path length measure at this particular scale:

$$l_T = n\Delta_T l \sim (\Delta_T l)^{-d} \Delta_T l = (\Delta_T l)^{1-d} \qquad (4.4)$$

Where: n = number of equal time segments path is divided into.

T = temporal scale at which we want to measure path length.

$\Delta_T l$ = expected displacement during time T (length scale)

l_T = total path length

d = estimated fractal dimension (based on the fitted slope of the relationship between $\Delta_T l$ *and* l_T on a log-log plot)

This plot should expose spatial domains where the forager changes movement patterns in response to the landscape features.

A purely fractal object is characterized by a single value of D, over all spatial scales. Hence, the object looks the same at all spatial scales (e.g. Koch snowflake) and we say that such objects are self-affine. Although many objects in nature are approximately fractal like (characterized by a single D), many natural processes "appear" fractal over a narrow range of spatial scales, but are not truly fractal. This is the case for many animal movement patterns, especially for larger animals and predators. It is also unfortunate that a number of studies have erroneously applied such methods and, hence, drawn incorrect conclusions (Turchin 1996). However, with careful application of the fractal method, it is possible to determine transitions in animal movement at certain spatial scales in response to a variation of landscape features at corresponding scales.

More specifically, Wiens (1989) defined "domains" of scale as regions dominated by a particular set of factors, separated by zones of transition. By being able to identify these transition zones and studying how animals react to the landscape within different domains, we are able to obtain movement information with respect to both spatial scale and spatial heterogeneity (Nams 2005). If the measure of path tortuousity does not

change with spatial scale than we can say that the path is fractal (Mandelbrot 1967, Nams & Bourgeois 2004). It is important to note, however, that to use the fractal dimension as an appropriate measure of path tortuousity, it must be established beforehand that the value for *D* does not change with differences in spatial scale over the entire path length (Turchin 1996). In circumstances where movement paths exhibit a value for *D* that does change, for instance in a CRW, tortuousity would be considered scale-dependent as it increases with spatial scale. For this reason, Turchin (1998) suggests using a CRW as a null model for animal movement and only considering fractal analysis if the movement pattern diverges from this.

Although there have been multiple studies of animal movement conducted, over a wide range of species (e.g., cabbage butterflies; Kareiva and Shigesada 1983, spider monkeys; Ramos-Fernández et al. 2004, reindeer; Marell et al. 2002 and caribou; Bergman 2000), there remains to be a general lack of knowledge about how these movement patterns may be affected by the heavily fragmented landscapes of urban environments. As urban development continues to grow around the world, more and more species are forced to adapt to the challenges of city life. One of the most obvious of these challenges being the disjointed distribution of resources in urban areas. By understanding how animals move through their home range, we may be able to better comprehend how animals interact with its environment. Movement patterns have important implications for the optimization of foraging strategies, habitat selection,

territorial and social behaviour and the implementation of successful management plans (Bascompte and Vilà 1997, Benhamou 2004, Doerr and Doerr 2004, Johnson 2005).

The red fox (*Vulpes vulpes*) is among the most successful species to colonize urban areas around the globe (Harris and Baker 2001). Although there exists an extensive body of literature surrounding urban foxes in Europe, investigating aspects of spatial organization such as home range (White et al. 1996, Baker et al. 2000, Doncaster and Macdonald 1991), dispersal mechanisms (Harris et al. 1988, Trewhella et al. 1988) and the potential spread of zoonotic diseases (Anderson et al. 1981, Hofer et al 2000), we lack information pertaining to what search strategies are being employed to obtain resources in urban environments.

As discussed in previous chapters, Charlottetown, the capital city of Prince Edward Island (PEI), Canada, has an abundant urban red fox population due to the immigration and establishment of coyotes to the island in the mid-1980's. Although the abundance of urban foxes is still unknown, evidence provided by the PEI Department of Forests, Fish and Wildlife, suggests that the number of urban foxes has increased over the last decade. The perception of red foxes in Charlottetown varies among residents from those who dislike the presence of the animal or are afraid of them, to those residents who feed them on a regular basis with the hopes of the animals returning to their properties. Such close contact between humans, domestic animals and foxes leads to unnaturally bold wildlife and an increased risk of disease and parasite transmission. With a greater knowledge of the foraging strategies being utilized by Charlottetown's foxes, we may be

able to gain a better understanding of how urban infrastructure and habitat fragmentation are affecting the decision making processes of urban wildlife and in turn altering movement patterns.

Therefore, the overarching goal of this study was to investigate the effects of confinement on the movement patterns and search strategies of urban red foxes both spatially and temporally in Charlottetown. Other objectives include investigating site fidelity patterns of foxes in urban areas and gaining information about resource patch size and residency time within these patches. We expect to observe differences in movement patterns based on the season in which the data was collected. In the winter, for instance, due to cold temperatures and snow accumulation, we anticipate larger movement bouts and Lévy-like patterns assuming food resources will be harder to find. We also presume there will be differences detected in male and female movement patterns based on seasonal and behavioral roles assumed by each.

4.3 Materials and Methods

4.3.1 Study Area

Charlottetown is the capital city of Prince Edward Island (PEI), as well as the largest urban area in the province with a population of 43,130 (PEI Statistics Bureau 2014) and an area of 67.4 km^2 (PEI Department of Environment, Energy & Forestry, 2010). For this study, the adjacent town of Stratford is included in the study area as it remains to be the third largest community on PEI and lies in very close proximity to the

capital city. Therefore, Stratford will hence forth be included when discussing "Charlottetown" (see Figure 3.2.1) The Charlottetown area encompasses land along the southern shore of the province and is constrained by the Hillsborough and the North Rivers with much of the city being exposed to the Charlottetown Harbor. Urban development is prominent along the waterfront with suburban areas stretching to the east, north and west with pockets of commercial development towards the northern perimeter. Along with urban and suburban development, Charlottetown boasts over 158 parks and green spaces that make up an area over 2.2 km^2 throughout the city (City of Charlottetown 2014). Another prominent landscape feature in the city is the 0.65 km^2 of agricultural land belonging to an Agriculture Canada crops and livestock research station (Agriculture Canada 2014).

4.3.2 Live Trapping and Handling

Live traps were placed in open areas of Charlottetown or in residential backyards where fox activity had been confirmed by visual observation or the use of trail cameras. Verbal permission from landowners was obtained prior to trap placement. Trapping efforts and GPS data were collected between August and March of 2013 and 2014. Halford's, guillotine style trap box traps (76.2 cm height x 76.2 cm width x 182.9 cm length) made from a combination of steel mesh and plywood were set in areas where red foxes are observed frequently or there was a lot of evidence of fox use in the area (i.e., scat, trails, animal remains, den sites). The outside of the traps were camouflaged with spruce boughs and other natural material and the inside was also insulated with leaves,

soil and grasses from surrounding areas. The traps were baited with rabbit meat and checked twice per day. Bushnell Trophy Cam HD Max trail cameras, which took 1 min video clips, were set up at the trapping sites and triggered by detecting differences in ambient temperature of the area (i.e. detection of body heat), were also placed at trapping sites to gain insight into animal activity in the vicinity of the traps. If there was no sign of foxes near the trap after 7 days the traps were moved to new locations.

Captured foxes were anesthetized using Medetomidine (Dex Domitor; Zoetis, New York, NY, USA), 100mg/kg; intramuscular (IM) and Ketamine (Vetalar; Bioniche Animal Health, Laval Trie, QC, Canada), 100 mg/kg; (IM) and Atipamezole (Antisedan; Zoetis, New York, NY, USA), 100 mg/kg; (IM) (University of Prince Edward Island, Animal Care Protocol 13-014). A physical exam was conducted to assess sex, condition of teeth and body, length, weight and check pulse and respiration rate. Vital signs were continuously monitored throughout immobilization. National Band and Tag Co. steel ear tags (model # 1005-681), were attached to each ear for future identification. Four Sirtrack GPS/VHF collars with internal timed release (Model GWC171, 25mm wide, 120 g, Sirtrack, New Zealand) were used for the first portion of tracking (foxes M1, M2, F1). These collars record a GPS fix every 15 minutes for approximately 18 days and are equipped with a VHF component so that the animal can be tracked manually while wearing the collar and also to retrieve the collar after release. A Suretrak receiver by Lotek Engineering Co. (STR_1000 telemetry receiver) and standard Yagi Antennas are used to locate the collar via its VHF frequency. In addition three Lotek Wildcell SLG

(230g) collars were used which also recorded a GPS fix every 15 minutes (except for one which was every 30 minutes) for a period of 14 days (foxes F2, F3, F4) These collars used a ground station modem and SIM card to upload GPS fixes every 1.5 hours.

4.3.3 Movement Data Processing and Analysis

Movement data were analyzed using the Animal Movement Analysis Program (AMAP). This program was written and developed by Dr. Sheldon Opps (Physics Department, University of Prince Edward Island). First, data was downloaded either from the retrieved collar or from the ground station modem unit. Any time periods that were not successful in downloading a GPS location were removed. In order to ensure the accuracy of GPS locations (Both Lotek and Sirtrack collars have an optimum accuracy of 5-10 m), data was reviewed for locations which were produced via a high Position Dilution of Precision (PDOP). This PDOP value is a measure of satellite geometry and takes into account each satellite's location relative to the other satellites in the constellation. A high PDOP value indicates a lower probability of accuracy and therefore it was ensured that collar data from each fox consisted of at least 90 % of GPS points corresponding to acceptable values of PDOP (< 8). Data was then converted to Universal Transverse Mercator (UTM) coordinates and imported into AMAP as text files.

Discretizing animal movement paths, the process in which we treat animal movement as a series of discrete consecutive steps, is a practice that has been used by many researchers studying animal movement. Due to the nature of movement data collection, however, it must be known, that in many cases we may be measuring these

steps differently than the natural steps of the animal being studied (Nams 2013). For example, time-discretization, such that is used in GPS studies, assumes that a "step" is the distance measured between GPS fixes, whereas in actual fact, the natural step of that animal may be much smaller. Limitations with the battery life and cost of GPS technology may prevent capturing natural steps at very small spatial scales. This issue, although important, does not invalidate this type of analysis, but simply asserts researchers to fully understand the implications of using null models, such as CRW's, to test animal movement. For example, when CRWs are sampled at smaller spatial scales than the natural step of the animal turning angles may become autocorrelated (Turchin 1998, Nams 2013), but when sampled at a larger scale than the natural step it may appear that the animal is travelling shorter distances than expected (Nams 2006, Nams2013). Thus, in the case of a rejected CRW model, researchers must fully consider whether the type of sampling used affected these result prior to ascribing any biological mechanism to the behaviour (Nams 2013).

For the purposes of this study, a path was considered to be the complete spatio-temporal record of all the moves made by the fox in a 24 hour period. For each path, AMAP was used to calculate the total length (L), net-squared displacement (Rn^2), which calculates the squared distance between each GPS location in an individual's path and the individual's original location, and path tortuosity (t), which is the degree of twistiness of the path. The path metric that is perhaps of the most importance in movement analysis is the net-squared displacement (Turchin 1998). This metric essentially measures the spatial

extent of a system, and how much of that system has been explored by the random walker. Net-squared displacement is also useful in animal movement studies as it can be related to diffusion models, which are thought of as the standard treatments of moving systems as regards to space and time.

The angle at which the direction of movement changes from that of the previous movement, known as the turning angle, and the absolute direction of each move were calculated from each step. Correlation in the turning angles and move lengths were calculated at each sequential step away from the origin of the path, using associated autocorrelation functions (ACF) and runs tests. This is important, as a basic assumption of a CRW states that no autocorrelation exists in the turning angles or the move lengths (Kareiva and Shigesda 1983, McCulloch and Cain 1989, Turchin 1998). CRWs in particular are characterized by directional persistence and turning angles being concentrated around zero degrees (Turchin 1998). Rayleigh z-tests (Rayleigh 1919) are used with circular data to test for the significance of the mean direction. These tests were therefore employed to examine the uniformity of the turning angles within the movement paths of each fox. If the paths demonstrate uniformity, it is assumed/understood that the fox is not demonstrating directional persistence and each sequential step direction is randomly chosen. Conversely, turning angles which are concentrated around 0 degrees, indicate directional persistence in movement corresponding to correlated random walk patterns.

Often when recording the temporal/spatial coordinates for animal movement, the inherent nature of the measurement process gives rise to temporal/spatial correlations between movement segments. Such correlations are not "real" biological correlations, but rather artifacts of the measurement process. The problem with serial correlations of this kind is that one cannot apply standard statistical methods for analysis (Turchin 1998). More critically, we are then unable to compare field results with theoretical predictions (such as for the expected net-squared displacement based on predictions for a correlated random walk (CRW) which may rely on the independence of turning angles and move lengths). For example, in a particular habitat patch, maybe the fox did not move much (perhaps it was resting). Nonetheless, GPS coordinates would still be recorded every 15 minutes and these coordinates would not truly represent movement based on biological decision making (i.e., this would not represent the foraging behavior we are interested in, but a resting mode). With this type of behavior, we would expect the move lengths and turning angles to be highly correlated. For the purposes of this study, eliminating this type of serial correlation from movement data is known as path-filtration. If, after path-filtration processes, movement paths are still demonstrating correlations within the data, then the possibility of biological correlations must be considered.

Statistically, autocorrelation analyses followed the methods by Turchin (1998). Serial autocorrelation in turning angle was examined on a lag-by-lag basis where for each lag, all possible pairs of turning angles separated by lag *d* are placed into two categories. 1) *S* or same where turns are in the same direction, and 2) *O* or opposite where turns are

in the opposite direction. The measure of autocorrelation used is a ratio of *(S-O) / (S+O)*. This value is scaled from -1 (where no autocorrelation is present and all turns separated by lag *d* are in the opposite direction) to 1 (where high autocorrelation is present all turns separated by lag d are in the same direction). For the purposes of this study we designated autocorrelation values > 0.4 to indicate moderate to strong autocorrelation as determined by many statisticians (Lund and Lund 2015, Dancey and Reidy 2004, Slemamijed 2004). Similarly, serial autocorrelations in move lengths were examined on a lag-by-lag basis and were statistically tested for using an autocorrelation function that classifies move lengths into being either less than or greater than the mean move length. For both turning angles and move lengths significance is indicated when the error associated with autocorrelation values are greater than two standard errors away from zero. Although it is possible to conduct this analysis for both individual movement paths as well as pooled data, it is important to view pooled data with caution as there is potential that the patchiness of the environment, (i.e., each fox could be moving differently at the same lag depending upon the environment it is encountering each day) could cause artificial autocorrelation in turning angle and move length data (Nams 2005).

Graphical exploration along with path-filtration processes in AMAP were performed initially to eliminate artificial (serial) autocorrelation within the movement data to determine at which measure the paths become too small to provide statistically meaningful analysis. Path-filtration processes used in AMAP follow techniques suggested by Turchin et al. (1991), in which *n* steps are aggregated into one move if the

n-1 spatial position is no more than *x* cm away from the line connecting the beginning of the first step to the end of the last one. Values of *x* start small and increase until the issue of serial autocorrelation is minimized. Similar methods are used with turning angle sizes. It must be noted, however, that caution must be used when conducting this analysis, as adjusting raw movement paths in such a way may eliminate the ability to characterize the movement patterns by the frequency of turns. Because foxes may respond differently to their environment at different spatial scales depending on the structure of habitat features and the quality of resources available to them, each fox was assessed independently to determine what degree of path-filtration was appropriate. Several paths were investigated for each fox to assure consistency with values of *x* that were selected for analysis. We ensured that not more than 50% of the original number of data points were eliminated by the filtration process to prevent a loss of key information, while still excluding unnecessary data points. After path-filtration was applied, the new paths were graphically compared to the original paths to ensure they maintained similar form and spatial features.

Comparisons between field observations and theoretical predictions, based on the CRW, for the net squared displacement were conducted at both the step and path level for each fox to determine if there were differences in movement patterns at different spatial scales. At the step-level analysis, the observed net-squared displacement (R_n^2) was calculated at each lag, *n*, for each path. The mean net-squared displacement was then calculated as an average over all of the paths for each fox.

The expected net-squared displacement was calculated from the following equation (Kareiva and Shigesada 1983):

$$R_n{}^2 = nm_2 + 2m_1^2\left[\frac{(c-c^2-s^2)n-c}{(1-c)^2+s^2} + \frac{2s^2+(c+s^2)^{\frac{n+1}{2}}}{[(1-c)^2+s^2]^2}\, y\right] \qquad (4.3)$$

Where:

m_1 = mean move length

m_2 = mean squared move length

c = average cosine of the turning angle

s = average sine of the turning angle

$y = [(1 - c)^2 - s^2] \cos[(n+1)\alpha] - 2s(1 - c) \sin[n + 1)\alpha]$

α = arctan (s/c)

Bootstrapping was employed to statistically compare the observed R_n^2 calculated from field data with the expected R_n^2 derived from theoretical models. The bootstrapping method involves first pooling the turning angles and move lengths for each individual fox for the full time period that movement data was collected. The bootstrapping method involves generating large numbers of pseudopaths by randomly selecting absolute direction, turning angles and move lengths from the pooled empirical data. Confidence intervals at the 95 % level are then constructed by randomly choosing n paths, calculating R_n^2 many times, sorting the data and then discarding the largest 2.5% and the smallest 2.5% of the values (Turchin 1998). If the observed net squared displacement data falls below the expected for a CRW, then this would demonstrate sub-diffusive behaviour characterized by a Brownian random walk. If the observed net squared displacement

exceeds the theoretical prediction for a CRW, then the movement pattern is more likely characteristic of a Lêvy walk (LW) (Benhamou 2007). Path level analysis was done by log transforming the graph of net-squared displacement against the lag for each path. Regression analysis was then performed on each graph to obtain the slope (scaling exponent) of the line. The same process was used to determine the expected slopes based on the R^2 values predicted for a CRW. A two-tailed t-test was used to compare the slopes of lines obtained from field data to the slopes of lines produced by the theoretical CRW model. To determine if movement patterns were representative of a Lévy Walk (LW), the move length distribution was analyzed graphically. A LW has scale invariant properties that have a long-tail distribution as a result of a power-law relationship between path properties and successive steps (see equation 4.3).

In order to investigate potential scale-dependent shifts in movement as a response to landscape features at various spatial scales, fractal analysis was conducted using AMAP. Detecting these shifts in movement can be done by calculating the fractal dimension, *D* (Nams 2005). The fractal dimension yields a measure of path tortuousity that lies between 1 and 2, where $D = 1$ would describe a less tortuous path and $D = 2$ would describe a path that exhibits plane filling random movement with lots of turns. The fractal dimension is typically estimated using the "dividers" or "ruler" method (Mandelbrot 1967): dividers of varying sizes are stepped along the path to obtain measurements of path length using a different ruler lengths (see equation 4.4)

In addition to the conventional movement analysis methodologies that have been described above, we have devised a complimentary analysis to further explore areas of elevated point densities and the patterns of movement as regards to resource/ habitat patch use. The idea was to determine if there were particular areas where the fox movement tended to be more clustered, indicating a potentially higher density of prey, or alternatively, preferred areas for other important daily activities (e.g., den locations or rest sites). This analysis was completed using the GPS data collected for each fox, broken down into daily movement paths. Areas of elevated point densities were identified to be a group of GPS fixes ≥ 3 with distances between them being ≤ 20 m and defined as individual clusters following similar methods of Sand et al. (2005), although distances were scaled down to reflect the smaller canid and more confined movement within urban areas. The distance of 20 m was chosen based on the accuracy of the GPS fixes of the collar types. Both Lotek and Sirtrack collars have an accuracy of approximately 5-10 m. We chose double the maximum error as we wanted to ensure that movements were real and not simply resultant of GPS error. QGIS was used for this analysis and the land use of the each area of elevated point density was recorded along with how many points were within that cluster. The approximate area of each region of elevated point density was measured by creating a 100% minimum convex polygon around all of the points within each region using the ruler tool. Clusters that yielded an area of less than 30 m^2 were excluded from analysis to assure GPS accuracy. The time the fox spent within each cluster was determined by examining the time stamps associated with each GPS fix and

adding them together. The GPS time stamps were then placed in chronological order and gaps within the timeline were assumed to be times the fox left the cluster. We then created a density metric to allow us to compare the size of the patches compared to the number of points contained within that patch. Determining how many times the animal left the cluster and returned again, gave us an indication of site fidelity. We also divided the number of times the fox entered the patch by the number of points within the patch, again, to allow comparability between the different patches.

4.4 Results

As indicated in the methods section (4.3) a total of 6 foxes were trapped and tracked from August 2013-October 2014. GPS data was collected for each fox over a three week time period. Each 24-hour time period of GPS data, within these three weeks was treated as an independent (sample) movement path; however due to technical difficulties (e.g., satellite/GPS receiver issues) we were unable to obtain data for all 21 days for all individuals and, thus, we were able to obtain a total of 92 fox movement paths.

In total the net-squared displacement of all foxes in this study show a common pattern: where the first few steps of movement exhibit a higher net-squared displacement than the expected theoretical movement for a correlated random walk (CRW); however, as the number of steps increase, the net-squared displacement falls below that of the expected for a CRW. This is demonstrated for all of the foxes studied in this paper and

suggests that movement is sub-diffusive. The highest net-squared displacement is observed in individual M2 who was collared during winter months. The lowest net-squared displacement was observed in individual F2 who was collared in the early fall (Figure 4.1). The movement behaviour of the red fox (all individuals) differed significantly from that expected of a correlated random walk models (two-tailed t-test, $p < 0.001$). Rayleigh z-tests indicate that turning angles were not uniformly distributed for individual paths of M1 on October 20, 24, 25 and November 6 ($p < 0.05$), F1 on November 2 ($p < 0.05$), F2 on February 26, 27 and March 8 ($p < 0.05$), M2 on February 1, 5, 6, 11, and 13. Because Rayleigh z-tests indicated non-uniformity of turning angles on a relatively small number of days (13 of 92 in which data was collected) overall movement of Charlottetown's foxes appears to be more characteristic of a random walk.

M2 demonstrated the highest mean path length at 13452.66 m ± 1726.87 m as well as highest mean move length 157.63 m ± 1.29 m, and F2 demonstrating the smallest mean path at 4165.82 m ± 475.99 m along with the shortest mean move length of 85.86 m ± 1.25 m (Table 4.1).

Movement data for each fox was pooled over the (roughly) three week time period as well as examined at an individual path level. Pooled data for each fox showed similar trends in correlation for turning angles and with autocorrelation values dropping rapidly at a lag of 1 for both original and path-corrected data (Figures 4.3). Rayleigh z-tests indicate that turning angles were not uniformly distributed for individual paths of M1 on October 20, 24, 25 and November 6 ($p < 0.05$), F1 on November 2 ($p < 0.05$), F2

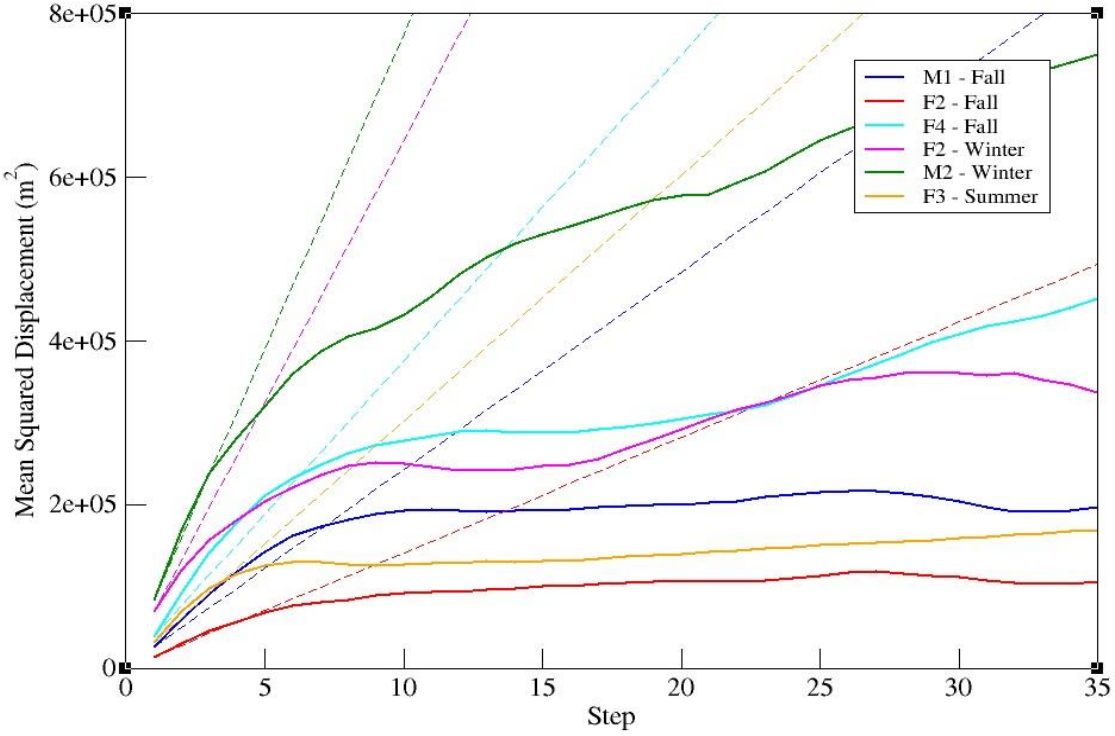


Figure 4.1. Comparison of the observed net squared displacement to that expected for a CRW for all foxes collared during this study with the solid lines indicating the observed CRW and the dashed lines representing the corresponding theoretical CRW for individual foxes. Note that each curve represents data pooled over a 2-3 week period for each fox.

Table 4.1. Average path characteristics for individual foxes, where each path corresponds to a 24-hr period in which the fox was collared and collecting GPS data. GPS fixes were taken every 15 minutes.

Fox ID	Number of Paths	Mean Path Length (m)	Error (m)	Mean Move Length (m)	Error (m)	Net Displacement (m^2)	Error (m^2)
M1	21	7869.45	±506.95	109.38	±1.31	175698.8	±40288.74
F1	10	4165.82	±475.99	85.86	±1.25	81671.82	±24199.57
F2*	13	5889.15	±350.01	128.4	±1.28	394740.79	±117578.51
M2	19	13452.66	±1726.87	157.63	±1.29	3372667.08	±1450293.01
F3	16	7696.64	±619.67	95.95	±1.26	240972.49	±34476.13
F4	13	9069.44	±552.59	109.47	±1.32	480958.15	±166316.15

* Time between GPS fixes was 30 minutes (i.e. move lengths = distance travelled in 30 mins).

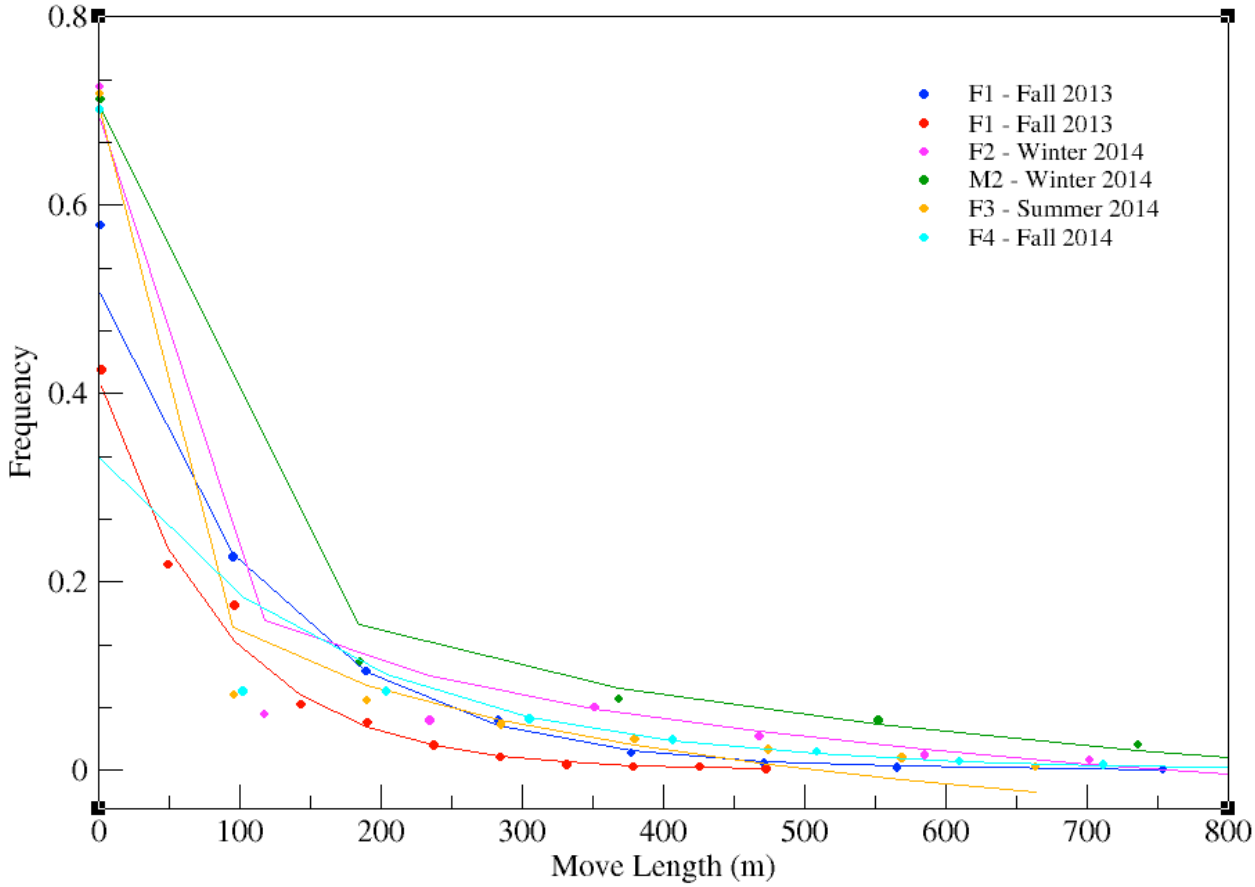
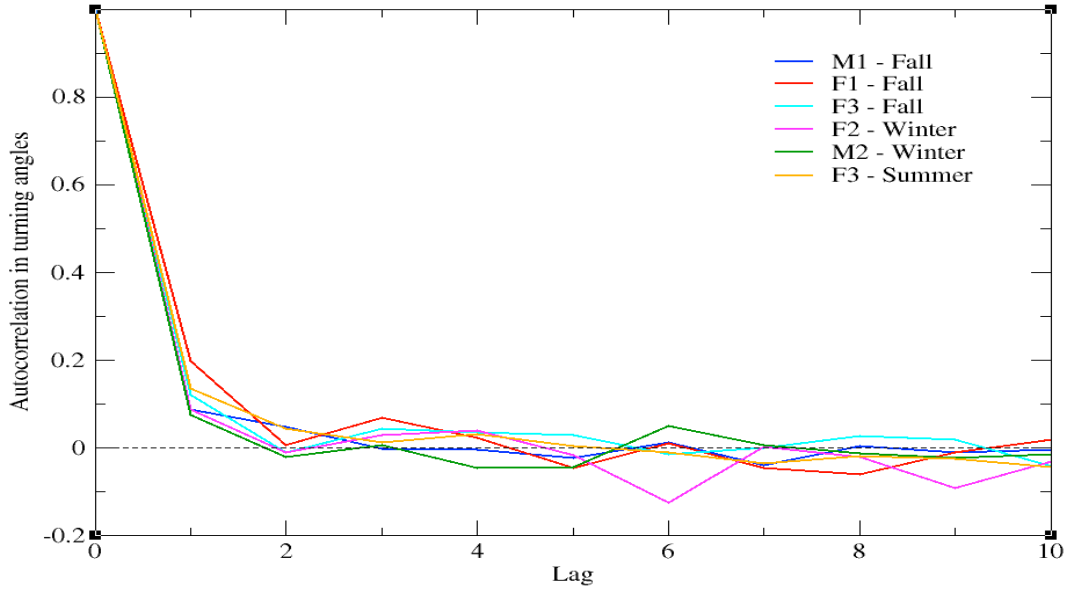


Figure 4.2. Move length distributions of red foxes in Charlottetown along with respective distribtion fits. M1, F1 and F4 (tracked in the Fall) all demonstarted exponential distributions. M2 and F2 (tracked in the winter) as well as F3 (tracked in late summer) demonstrated logarithmic distributions.

A)



B)

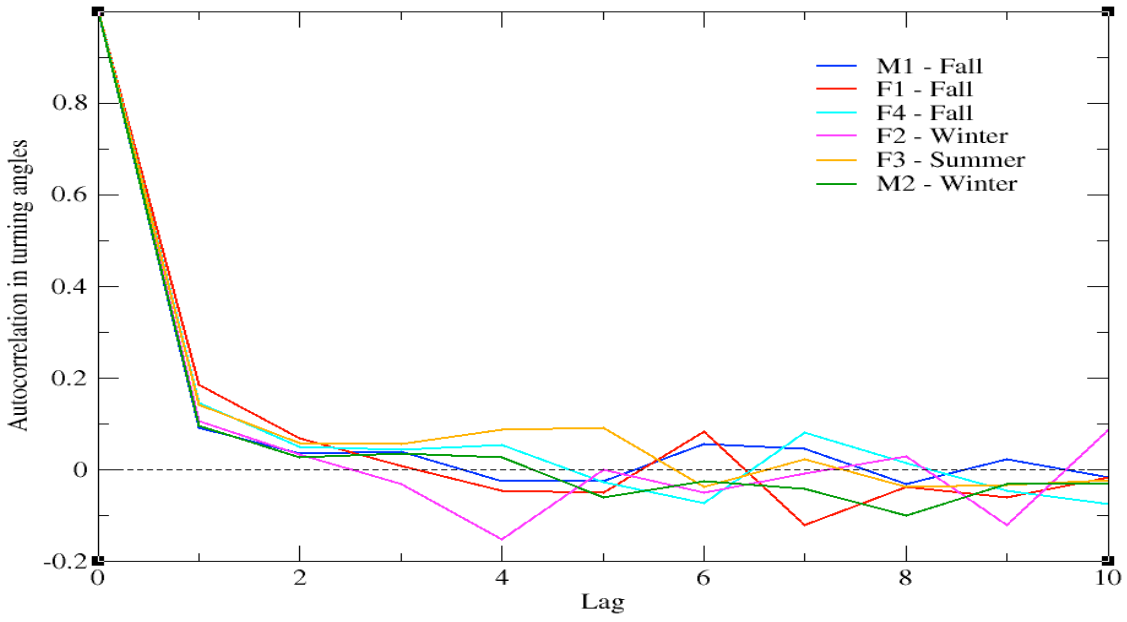


Figure 4.3. Autocorrelation analysis of turning angles for pooled data of individual foxes A) Original data B) After path-filtration processes.

on February 26, 27 and March 8 ($p < 0.05$), M2 on February 1, 5, 6, 11, and 13 ($p < 0.05$), F3 on August 4, 5, 9, 10, 12 and 16 ($p < 0.05$).

The non-uniformity of turning angles on multiple days for each fox may further indicate that the data does not fit a CRW model. Clear variation was graphically demonstrated in the autocorrelation values of both turning angles and move lengths of individual paths of each fox (Figures 4.4 – 4.6 for turning angles) and (Figures 4.8 – 4.10 for move lengths). Path-filtered data for individual movement paths of each fox were not included in this thesis as the differences, in comparison to those figures generated from the original data, were minimal. This suggests that our sampling frequency of 15 minutes was adequate for measuring urban fox movement in Charlottetown. This frequency was chosen as it allowed for fine scale movement to be recorded while still allowing a GPS collar battery life of at least two weeks. The high activity level of foxes observed by residents in Charlottetown prior to this study, despite the time of day, further motivated us to use a GPS frequency interval that would capture both nocturnal and diurnal movement events. Additionally, GPS fix intervals < 1.5 hours have been found to have higher fix success rates than longer fix intervals (Mills et al. 2006).

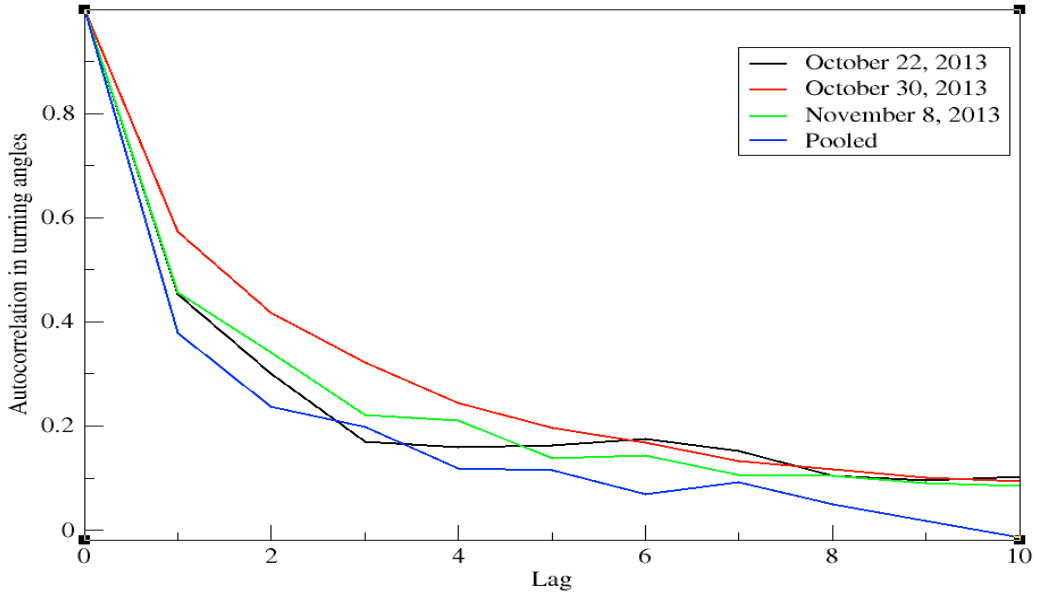
Fractal analysis demonstrated that movement paths of the foxes in this study were not self-similar (fractal) at the path level and yielded no obvious demarcation of movement transitions at smaller spatial scales.

Cluster size distributions for individual foxes all demonstrate similar patterns exhibiting a higher frequency of clusters at smaller sizes and logarithmic curve fitting

(Figures 4.11 – 4.13). Frequency distributions of the times spent in each cluster demonstrate the preference for shorter residency time to longer for all foxes with females spending longer amounts of time in one area (Figures 4.14 – 4.16). These histograms also demonstrate a logarithmic relationship between frequency and residency time.

Variation in the density of points within clusters (patches) as well as the relative entrance/exit rates of each cluster, demonstrated by individual foxes most likely reflects differences in the season the data was collected, the habitat composition of individual foxes and the different biological roles of males and females (Figures 4.17 – 4.20).

A)



B)

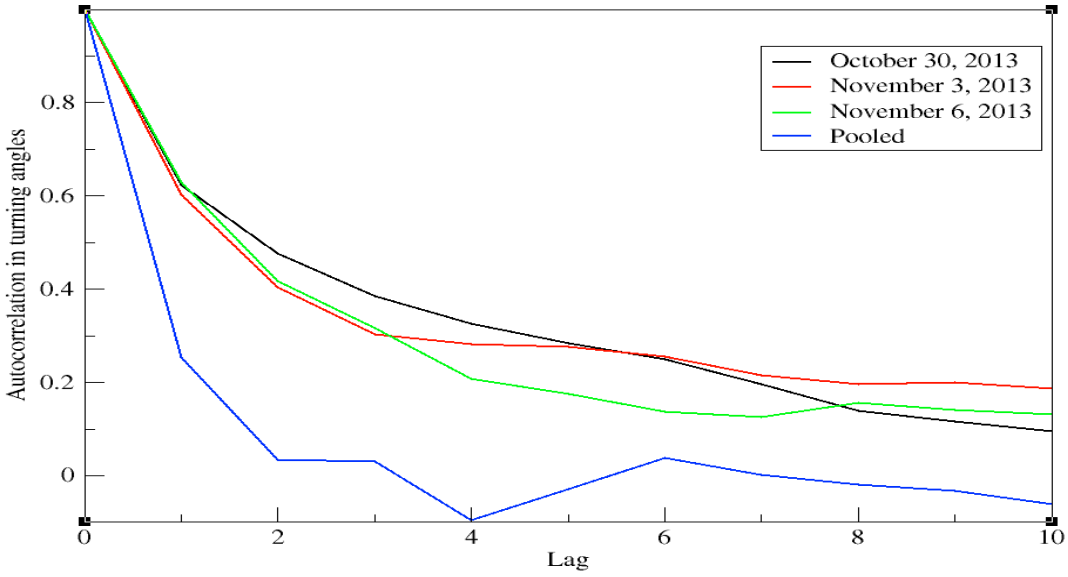
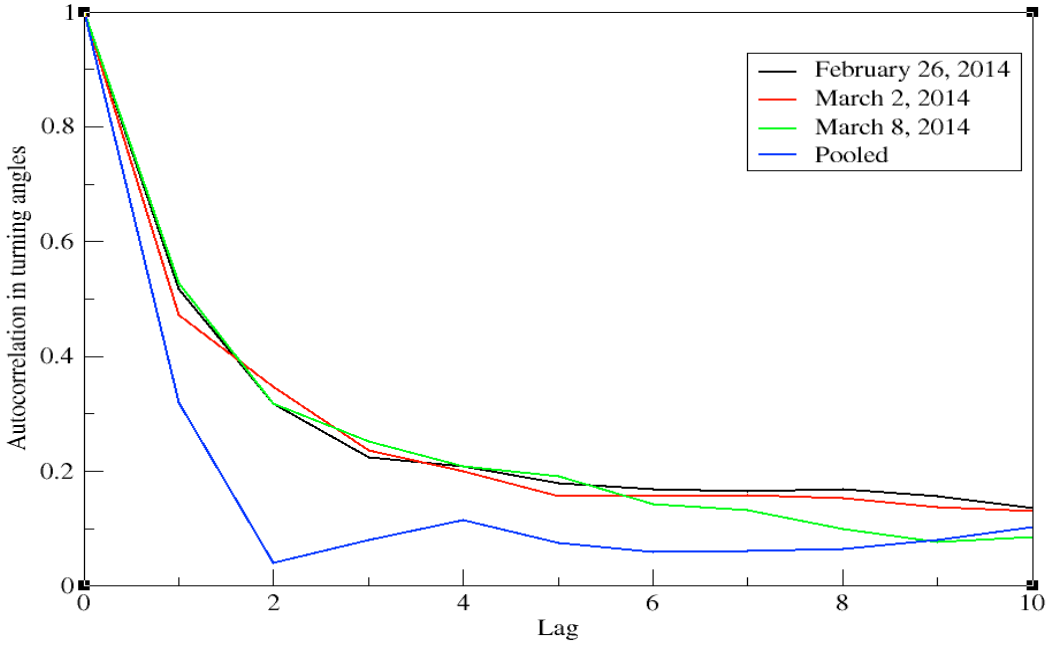


Figure 4.4. Autocorrelation analysis of turning angles for individual paths as well as that pooled data for A) M1 B) F1. Movement paths shown were chosen from beginning, middle and end of 2-3 week data collection period.

A)



B)

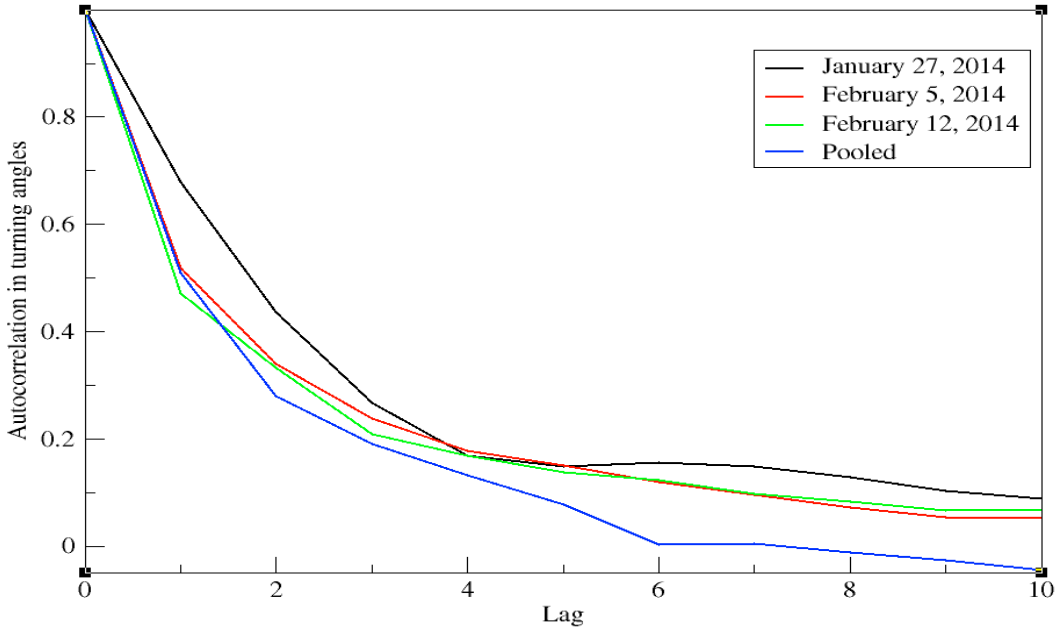
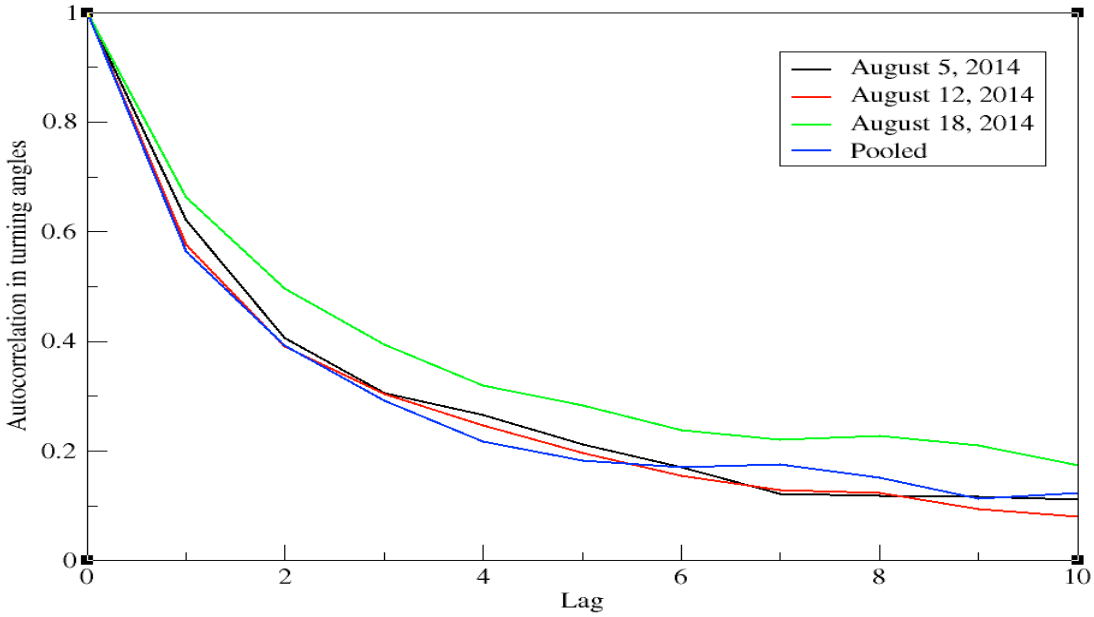


Figure 4.5. Autocorrelation analysis of turning angles for individual paths as well as that pooled data for A) F2 B) M2. Movement paths shown were chosen from beginning, middle and end of 2-3 week data collection period.

A)



B)

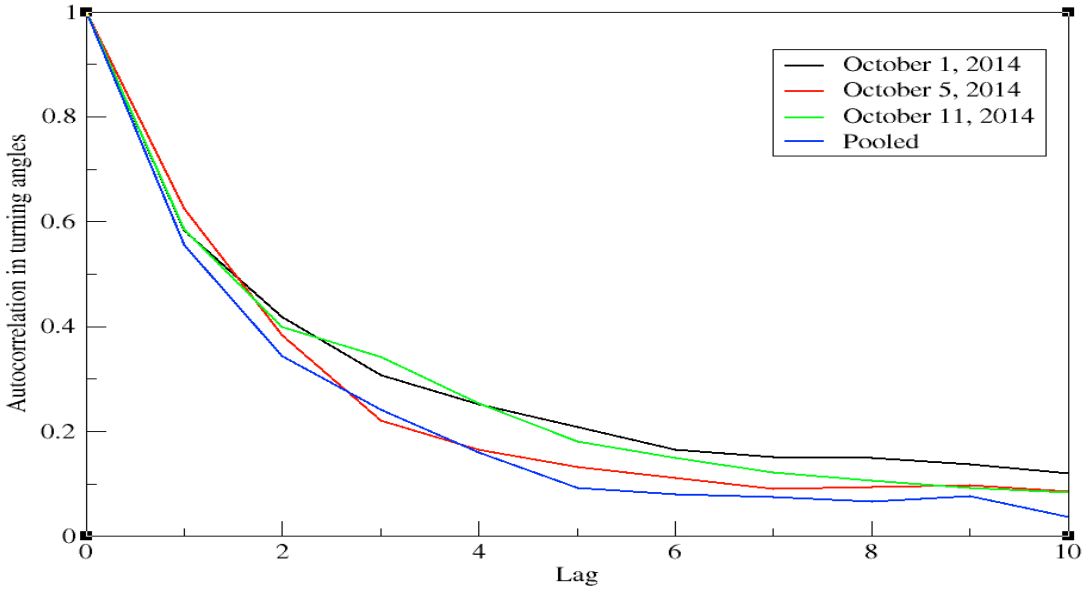
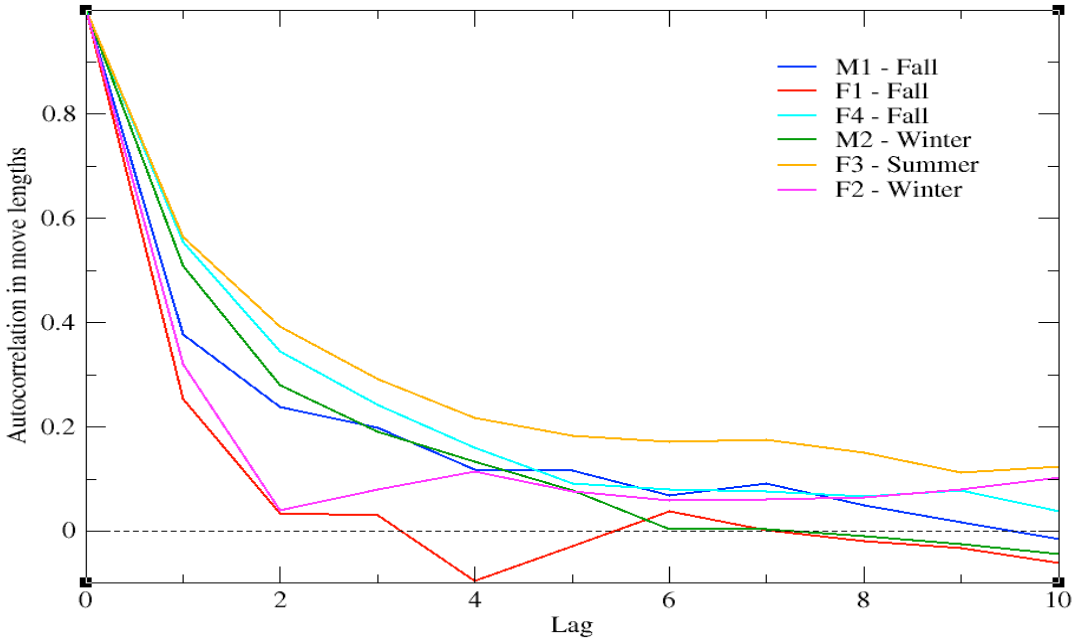


Figure 4.6. Autocorrelation analysis of turning angles for individual paths as well as that pooled data for A) F3 B) F4. Movement paths shown were chosen from beginning, middle and end of 2-3 week data collection period.

A)



B)

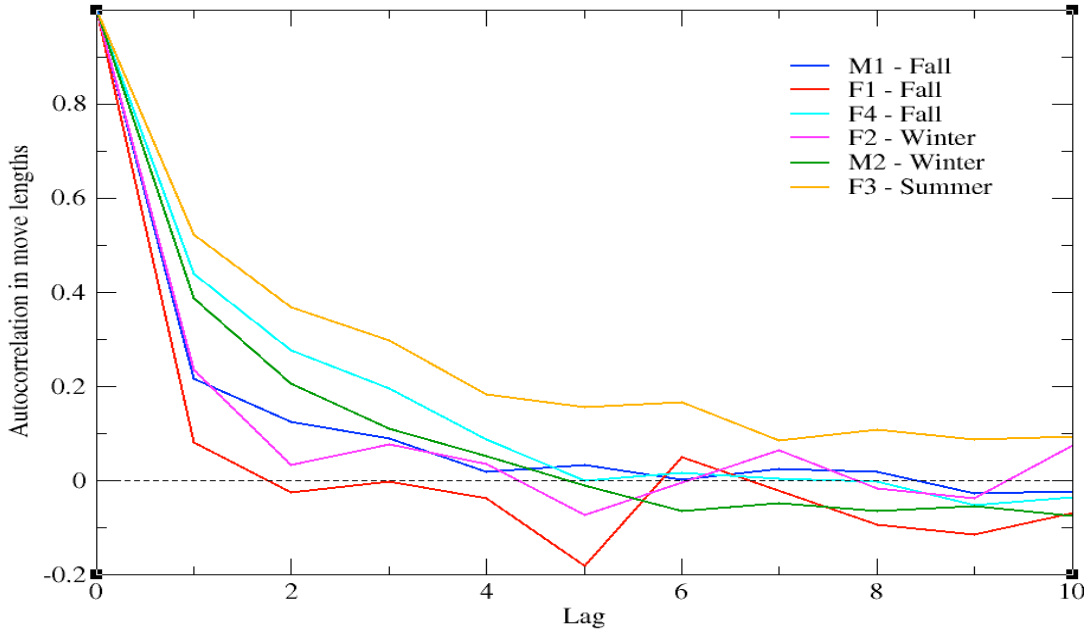
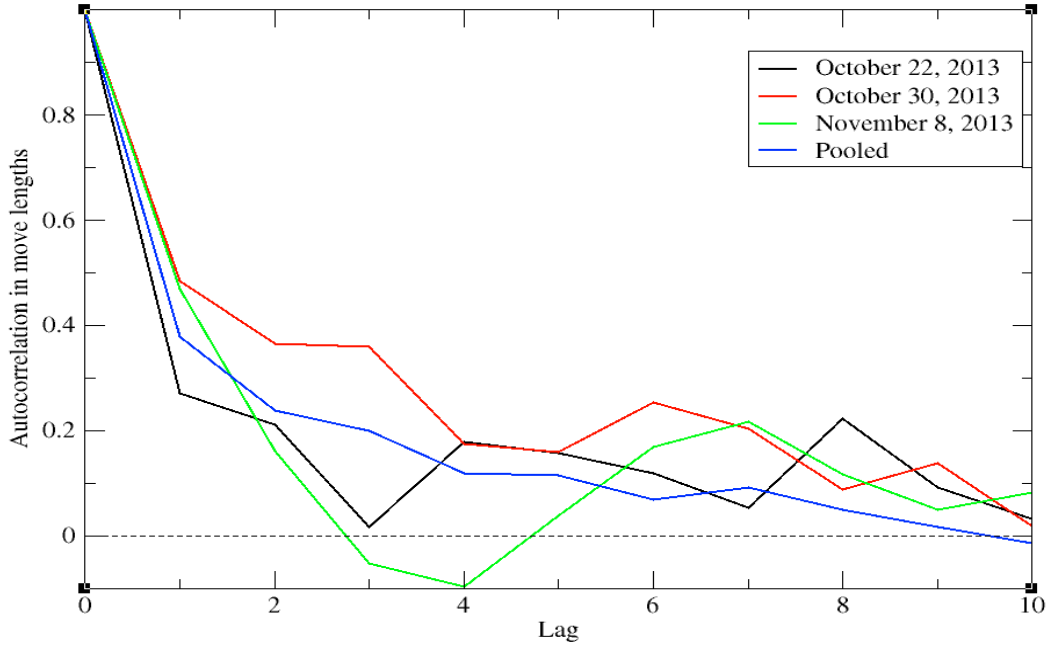


Figure 4.7. Autocorrelation analysis of move lengths for pooled data of individual foxes A) Original data B) After path-filtration processes.

A)



B)

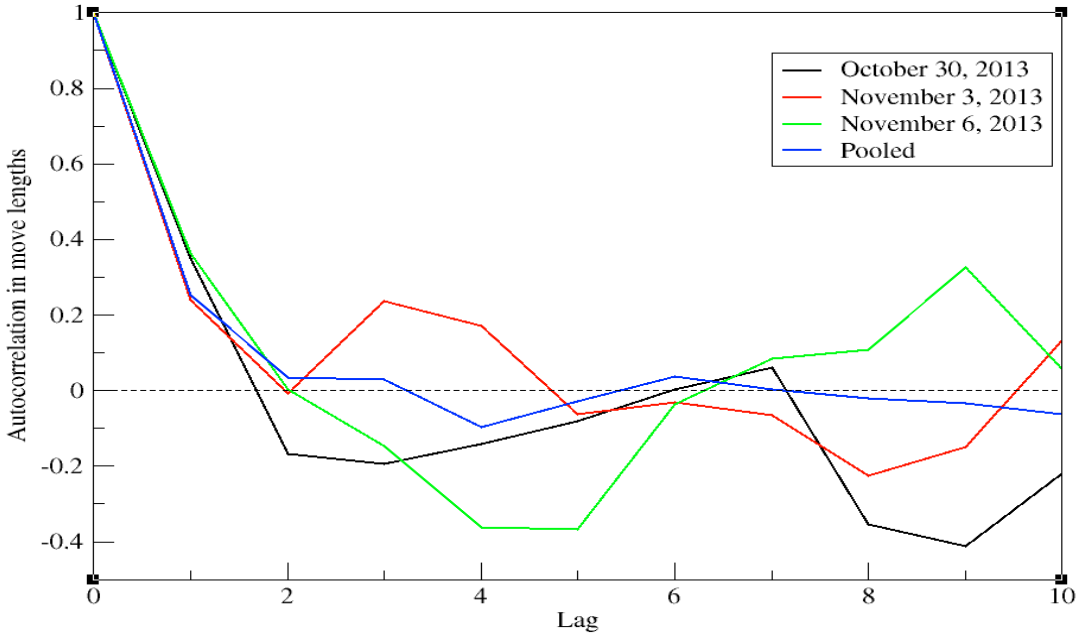
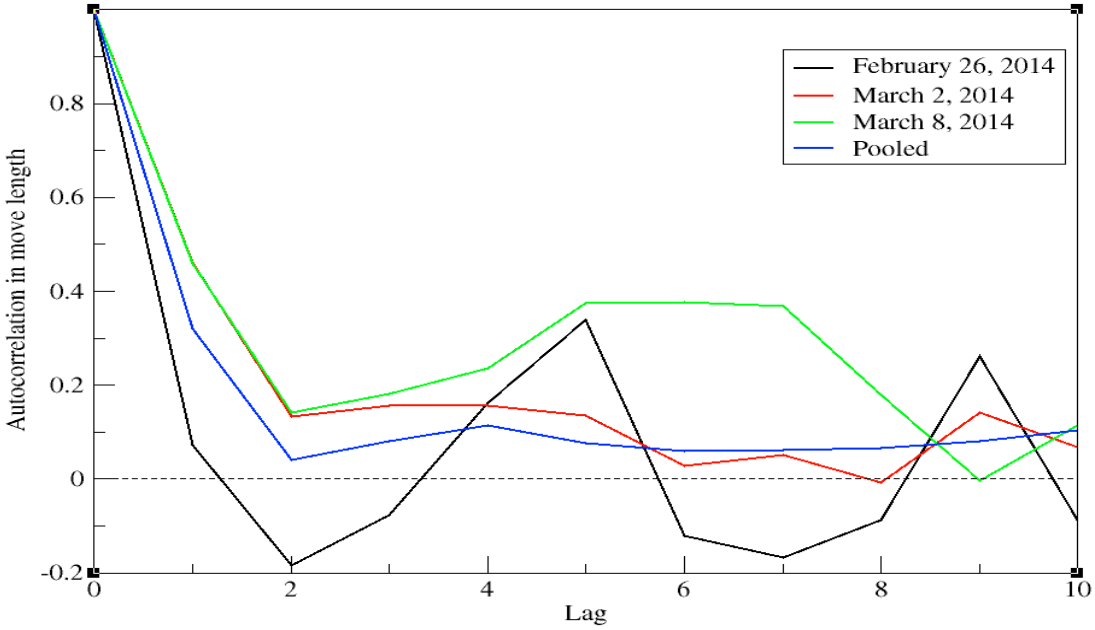


Figure 4.8. Autocorrelation analysis of move lengths for individual paths as well as that pooled data for A) M1 B) F1. Movement paths shown were chosen from beginning, middle and end of 2-3 week data collection period.

A)



B)

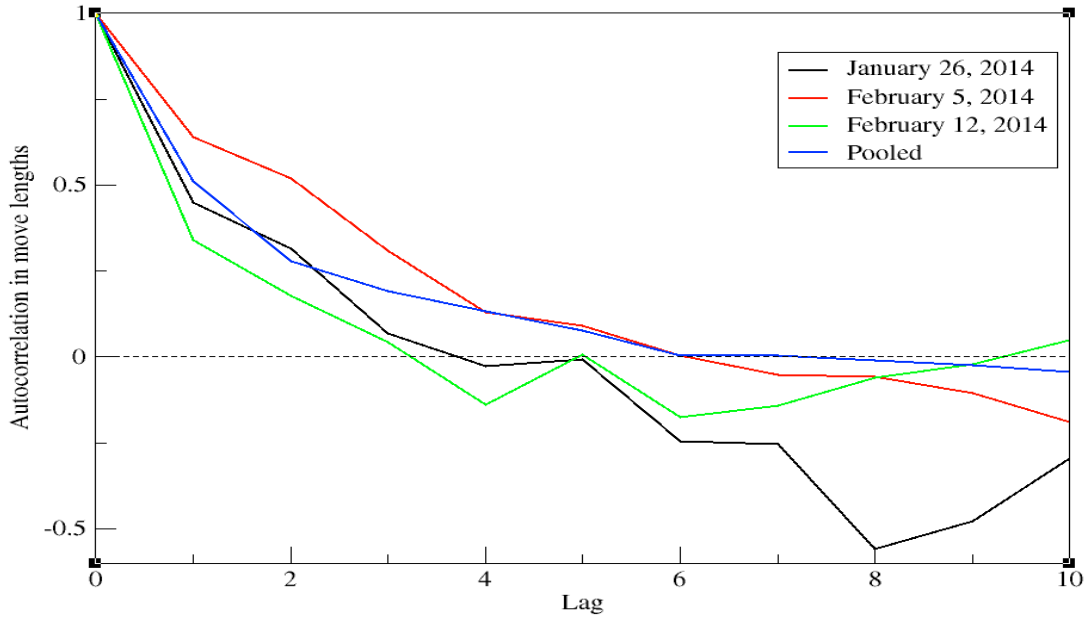
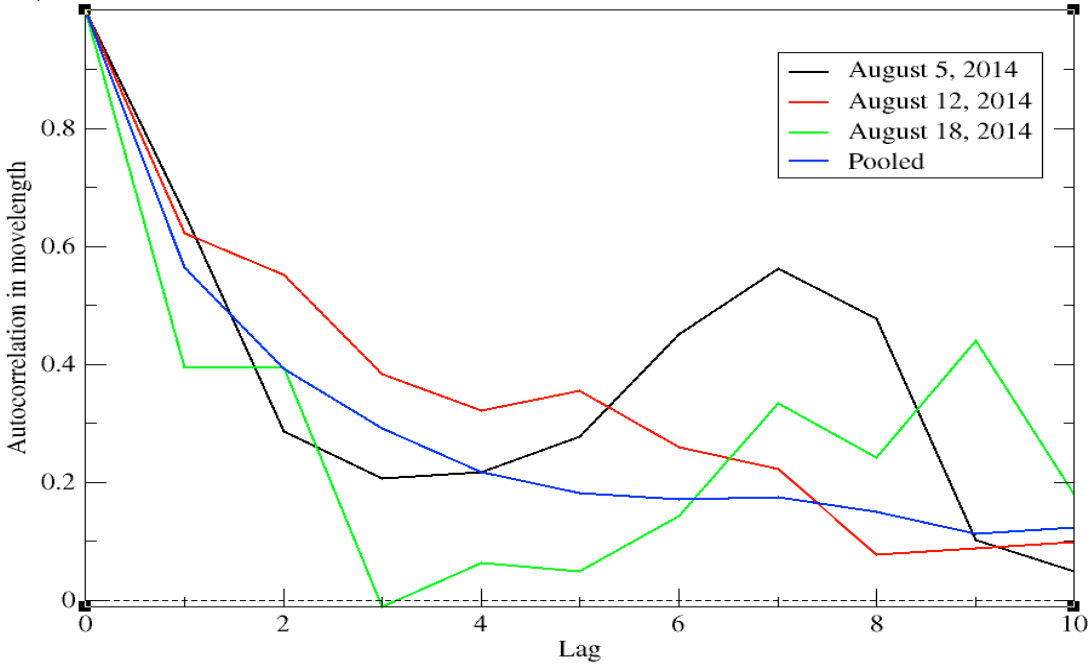


Figure 4.9. Autocorrelation analysis of move lengths for individual paths as well as that pooled data for A) F2 B) M2. Movement paths shown were chosen from beginning, middle and end of 2-3 week data collection period.

A)



B)

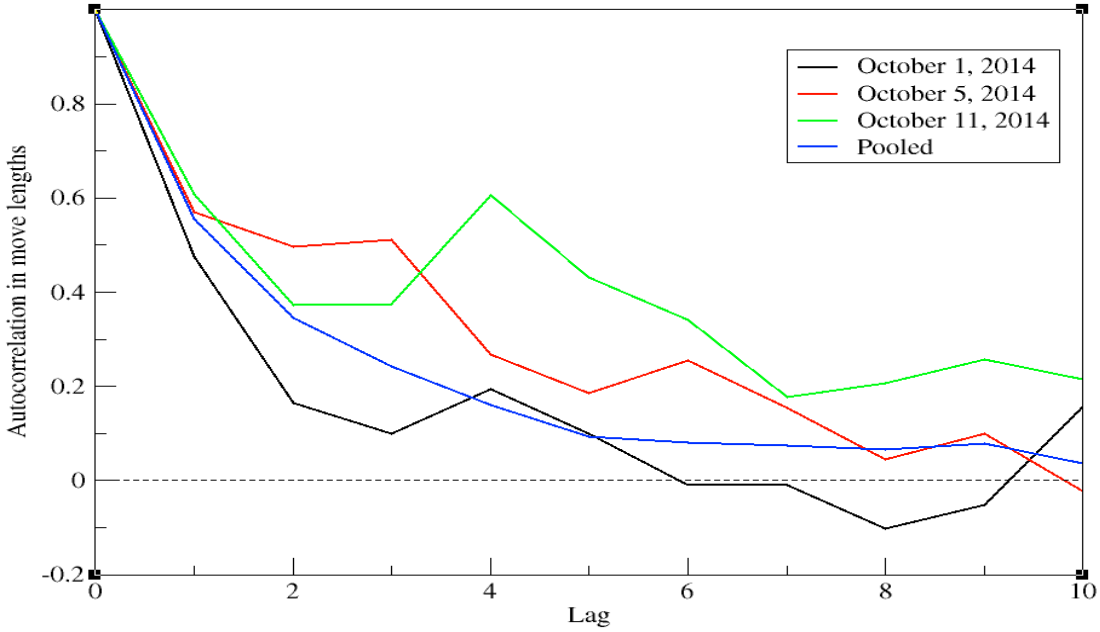
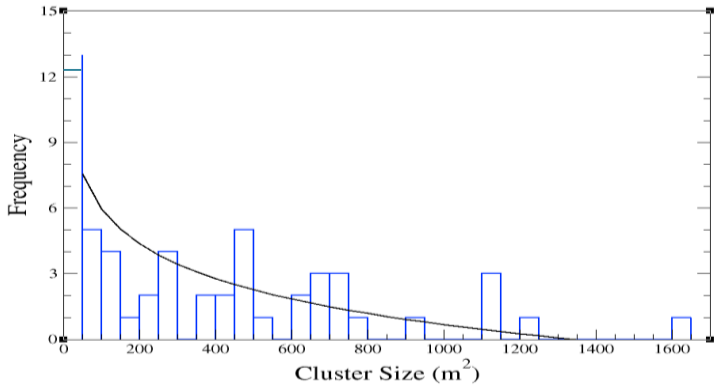
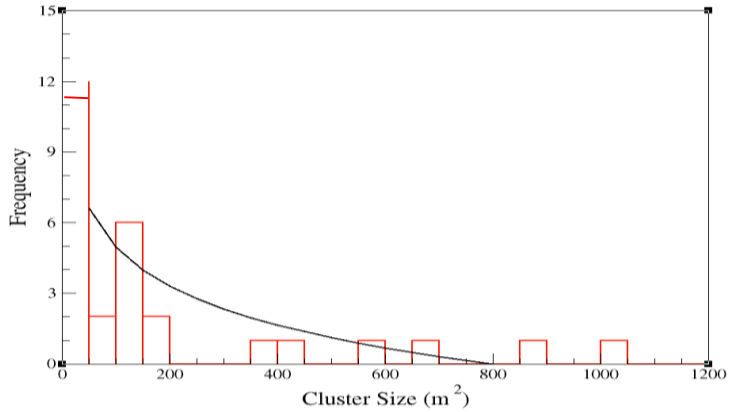


Figure 4.10. Autocorrelation analysis of move lengths for individual paths as well as that pooled data for A) F3 B) F4. Movement paths shown were chosen from beginning, middle and end of 2-3 week data collection period.

A)



B)



C)

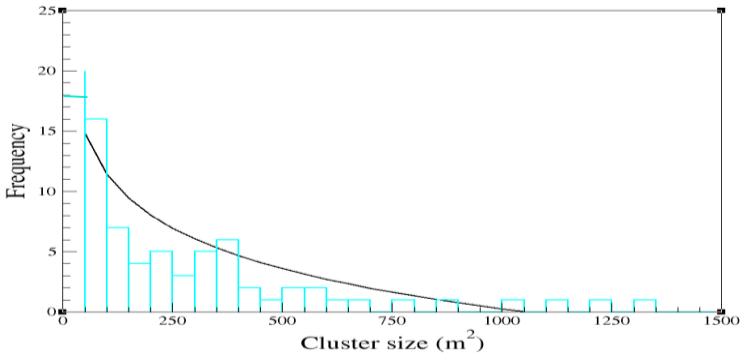
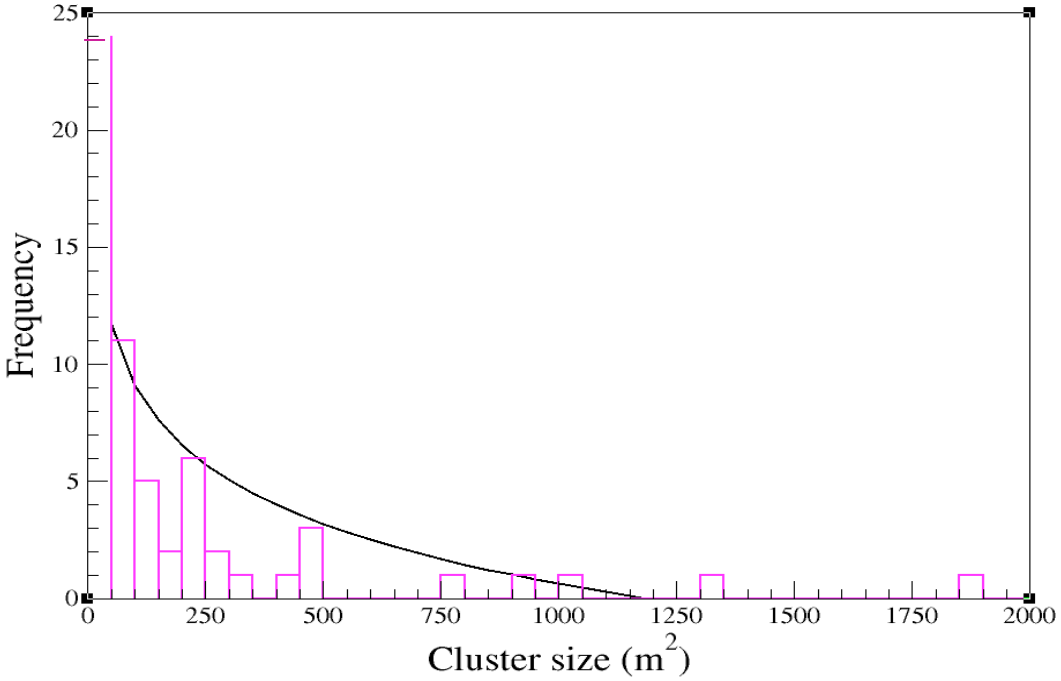
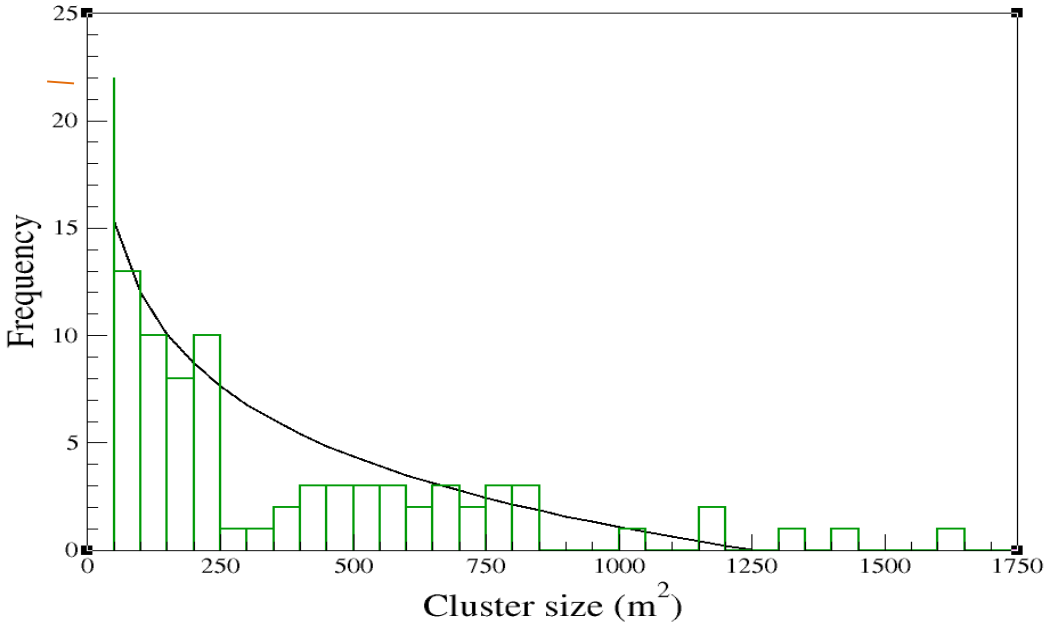


Figure 4.11. Cluster size distributions for foxes collared in the Fall of 2013 and 2014 along with logarithmic best fit curves. A) M1 (r^2 = 0.77) B) F1 (r^2 = 0.75 C) F4 (r^2 = 0.76

A)





B)

Figure 4.12. Cluster size distribution for foxes collared in the winter of 2014 with logarithmic best fit curves. A) F2 (r^2 = 0.76) B) M2 (r^2 = 0.88)

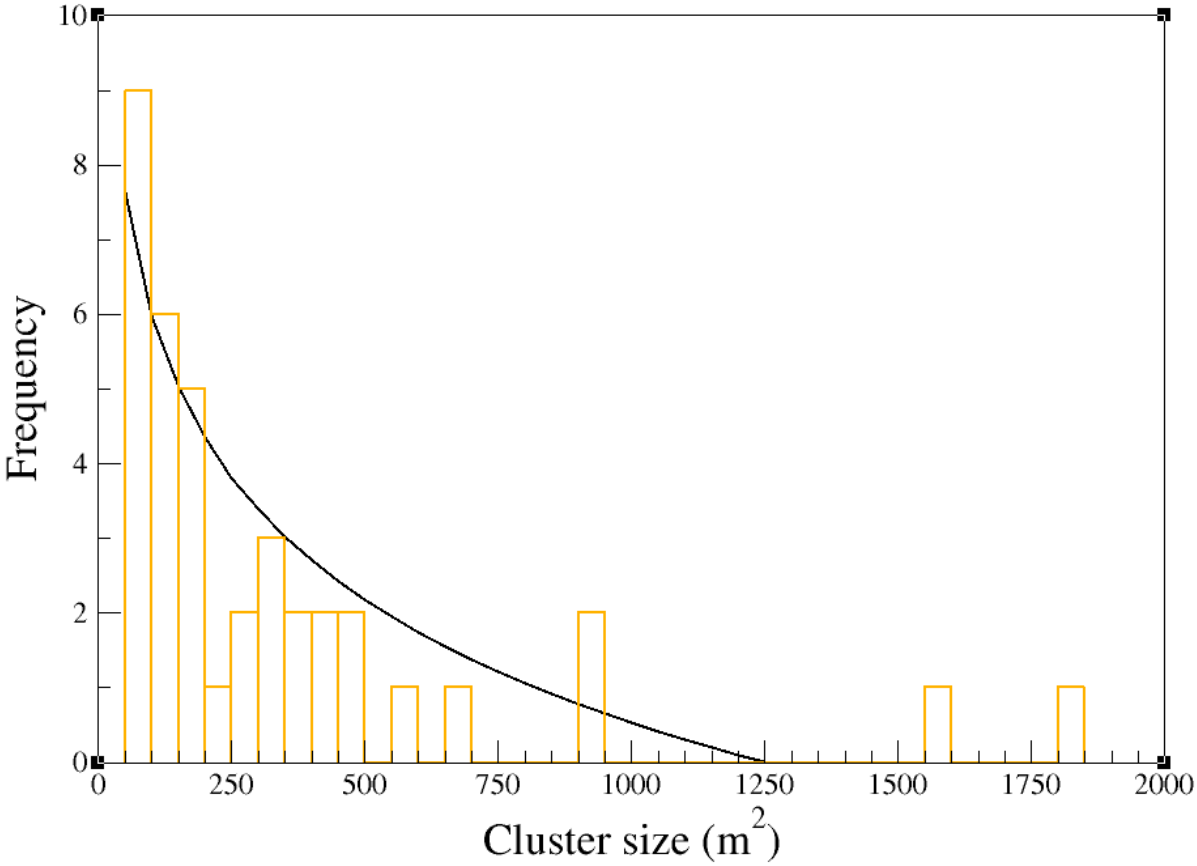
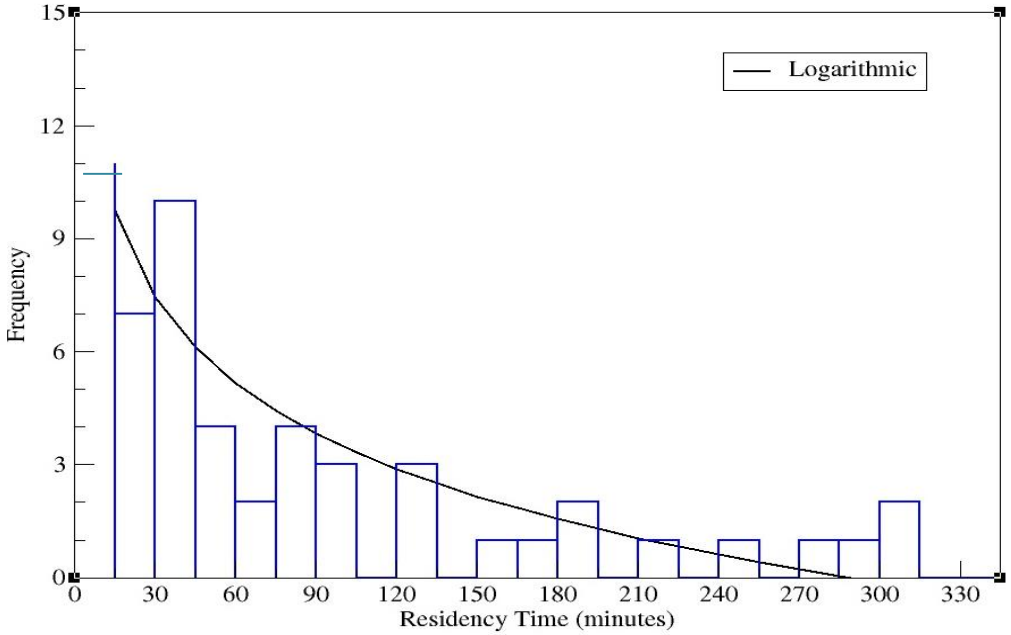


Figure 4.13. Cluster size distribution for fox, F3, collared in the summer of 2014 with logarithmic best fit curve ($r^2 = 0.88$).

A)



B)

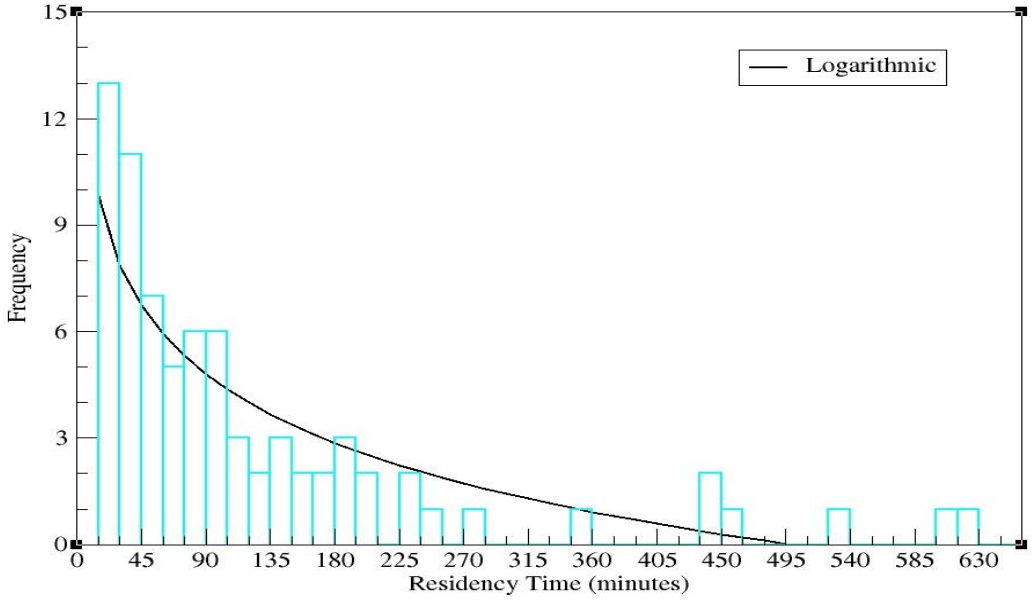
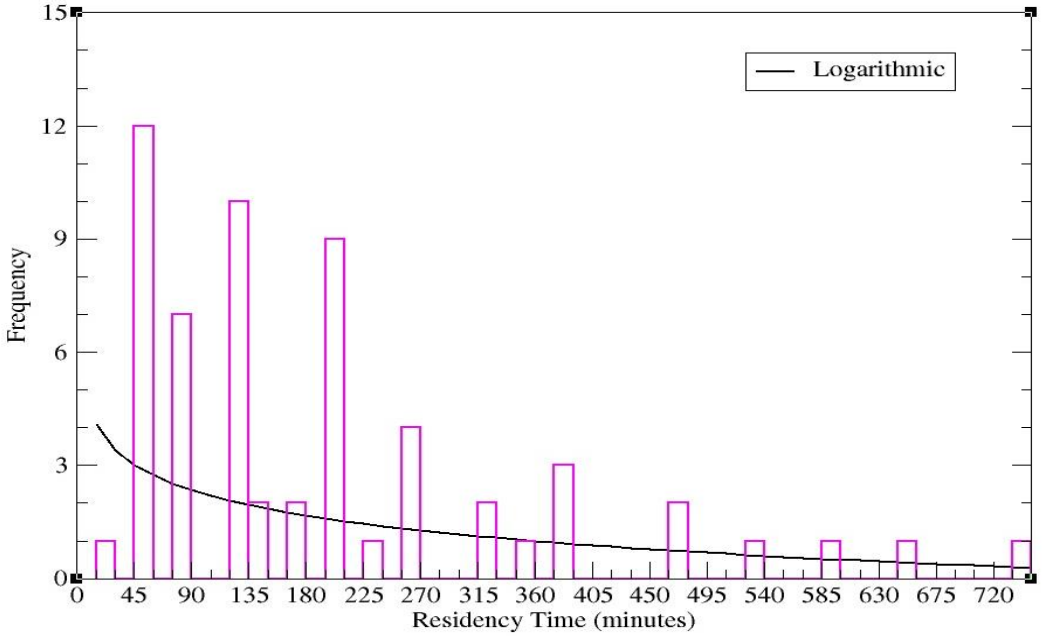


Figure 4.14. Residency time distribution of time spent in clusters (patches) for foxes collared in the fall of 2013 and 2014 with best fit curve. A) M1 ($r^2 = 0.88$) B) F4 ($r^2 = 0.84$).

A)



B)

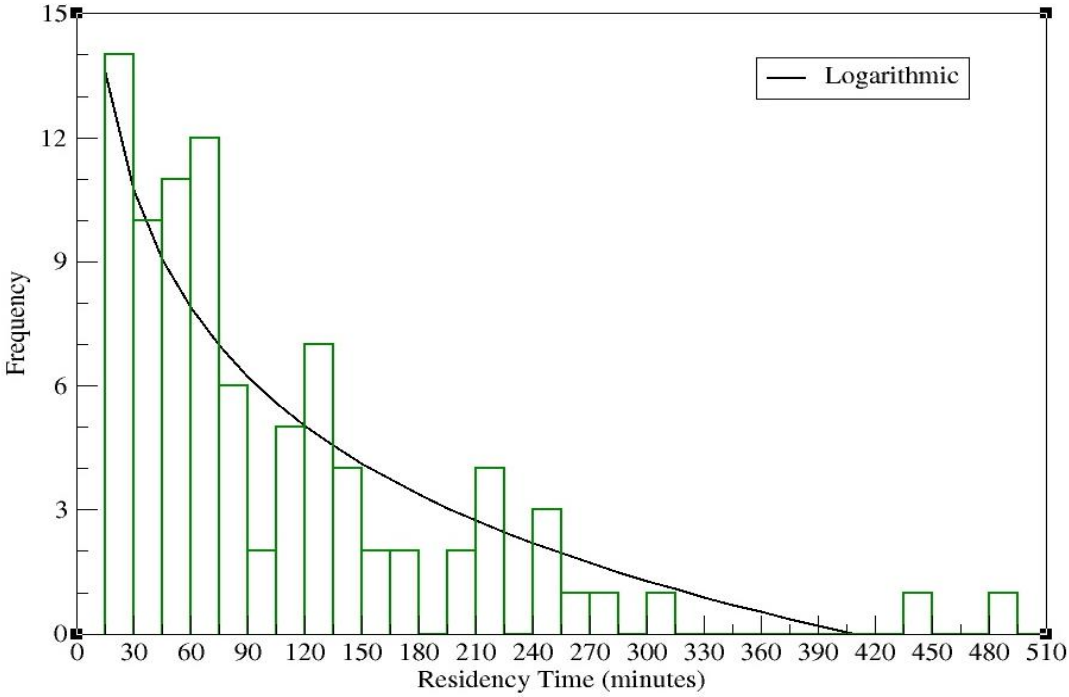


Figure 4.15. Residency time distribution of time spent in clusters (patches) for foxes collared in the winter of 2014 with best fit curve. A) F2 ($r^2 = 0.32$) B) M2 ($r^2 = 0.88$).

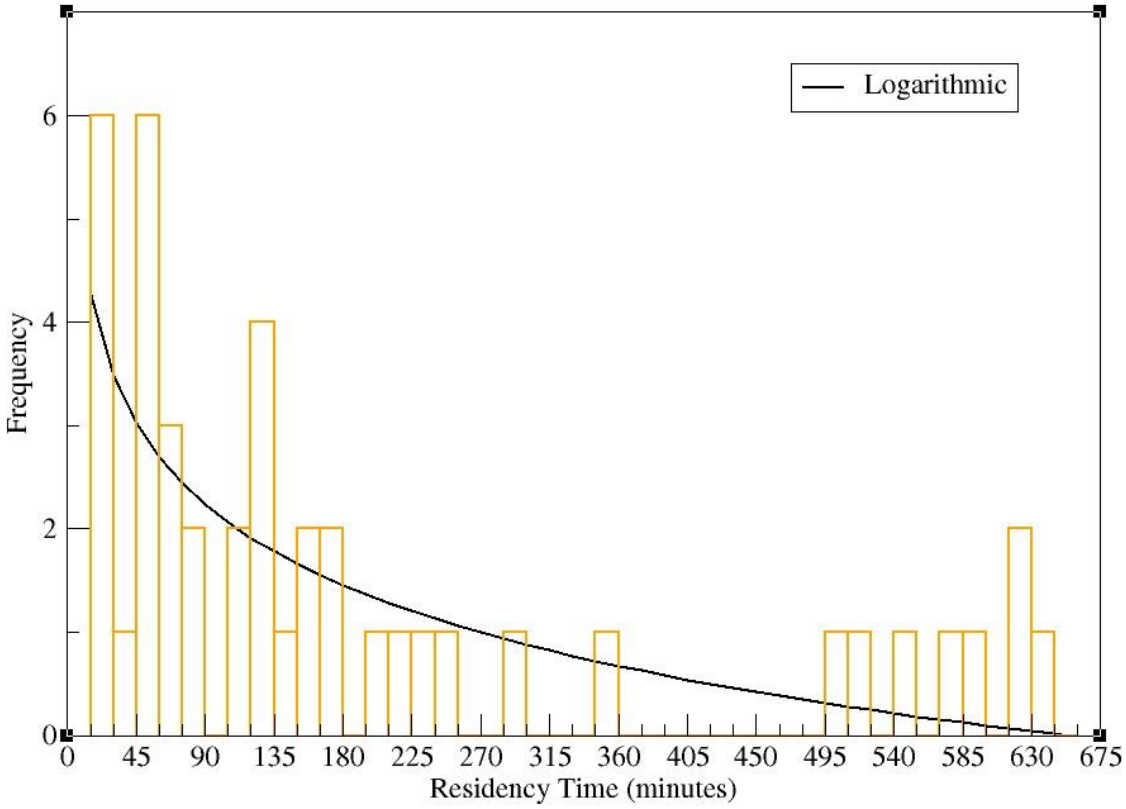
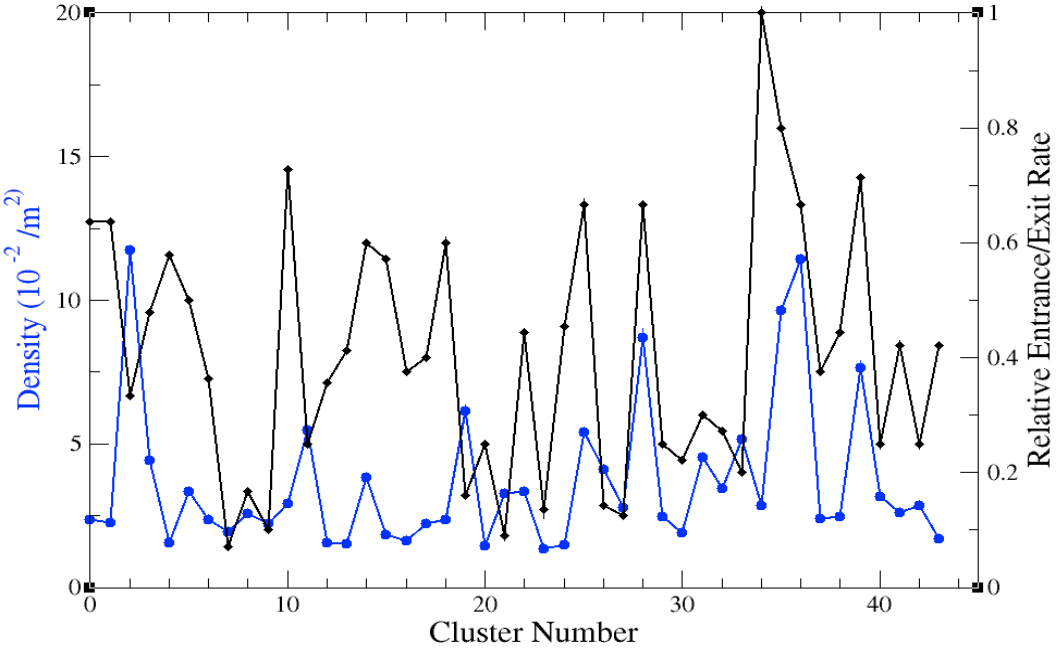


Figure 4.16. Residency time distribution of time spent in clusters (patches) for fox, F3, collared in the summer of 2014 with best fit curve ($r^2 = 0.68$).

A)



B)

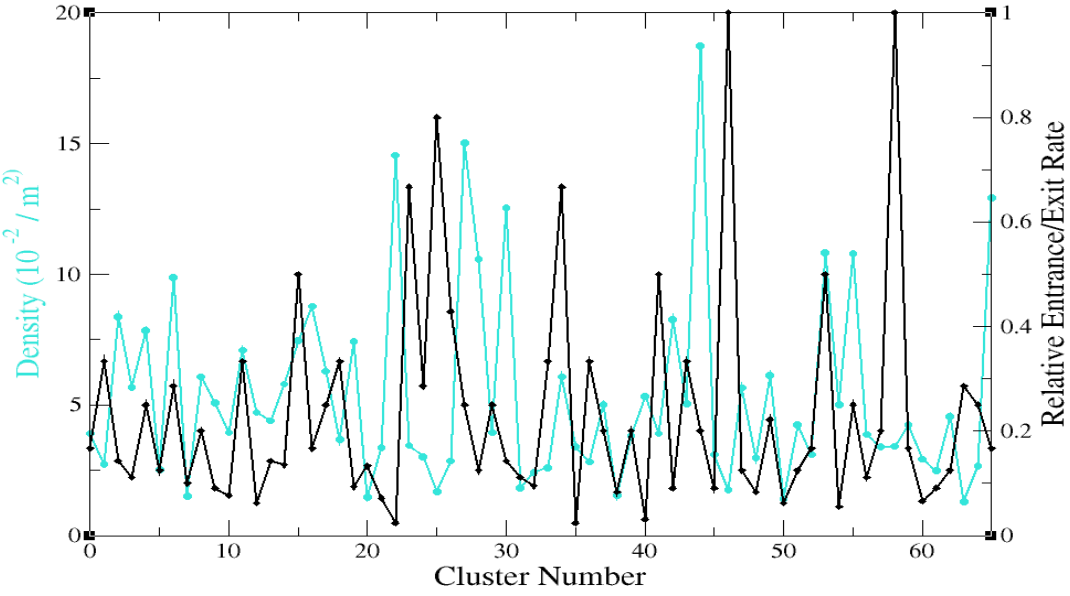
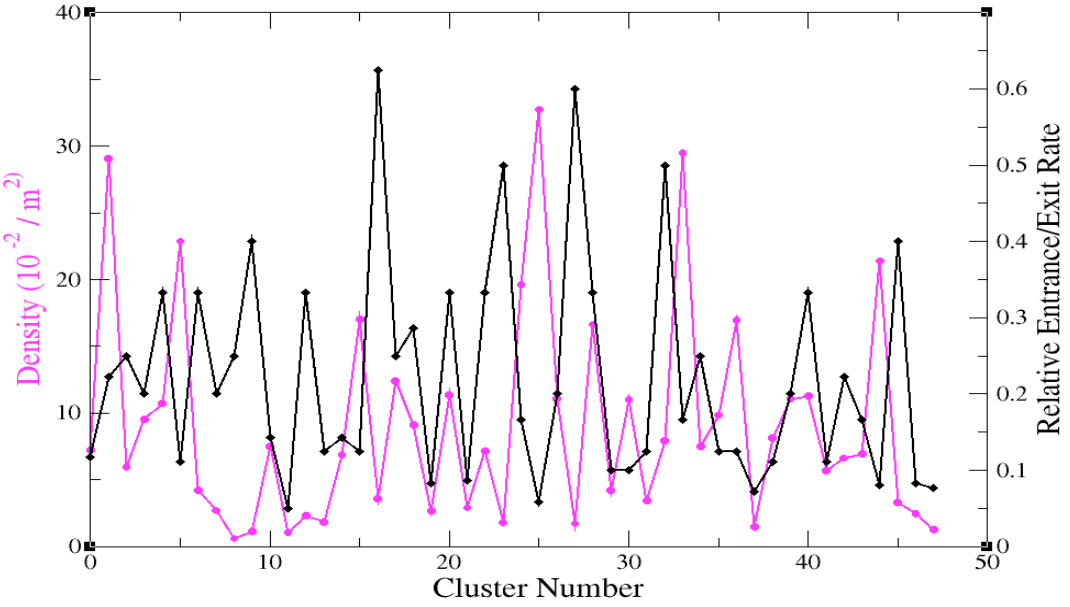


Figure 4.17. The density (10^{-2}/m^2) of points within a cluster in relation to the amount of times the fox exits and returns to that cluster (flux rate) for foxes collared in the fall of 2013 and 2014 A) M1 B) F4.

A)



B)

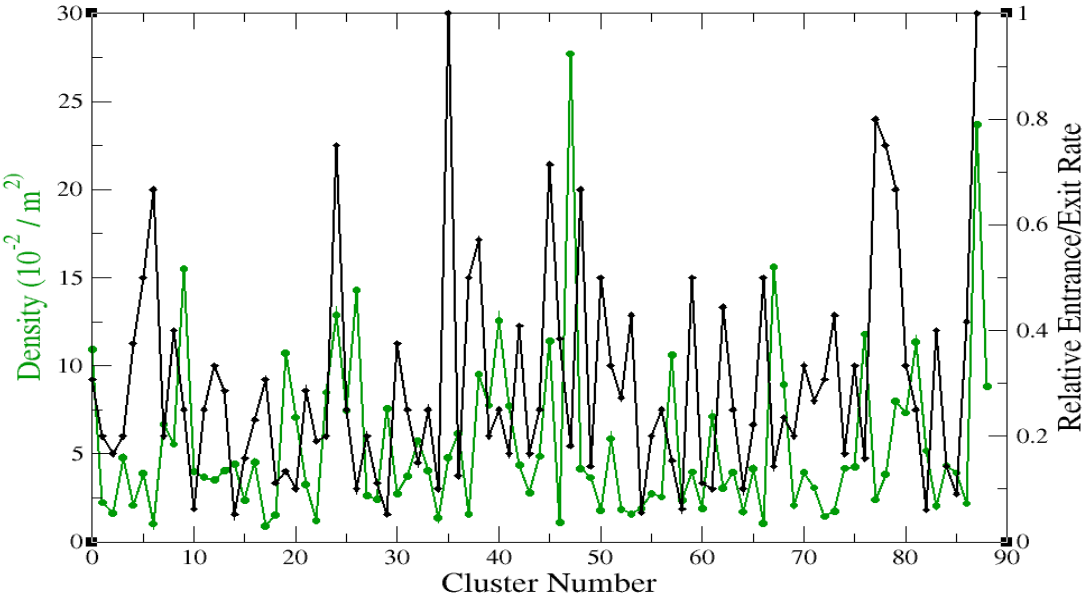


Figure 4.18. The density (10^{-2}/m^2) of points within a cluster in relation to the amount of times the fox exits and returns to that cluster (flux rate) for foxes collared in the winter of 2014 A) M2 B) F2

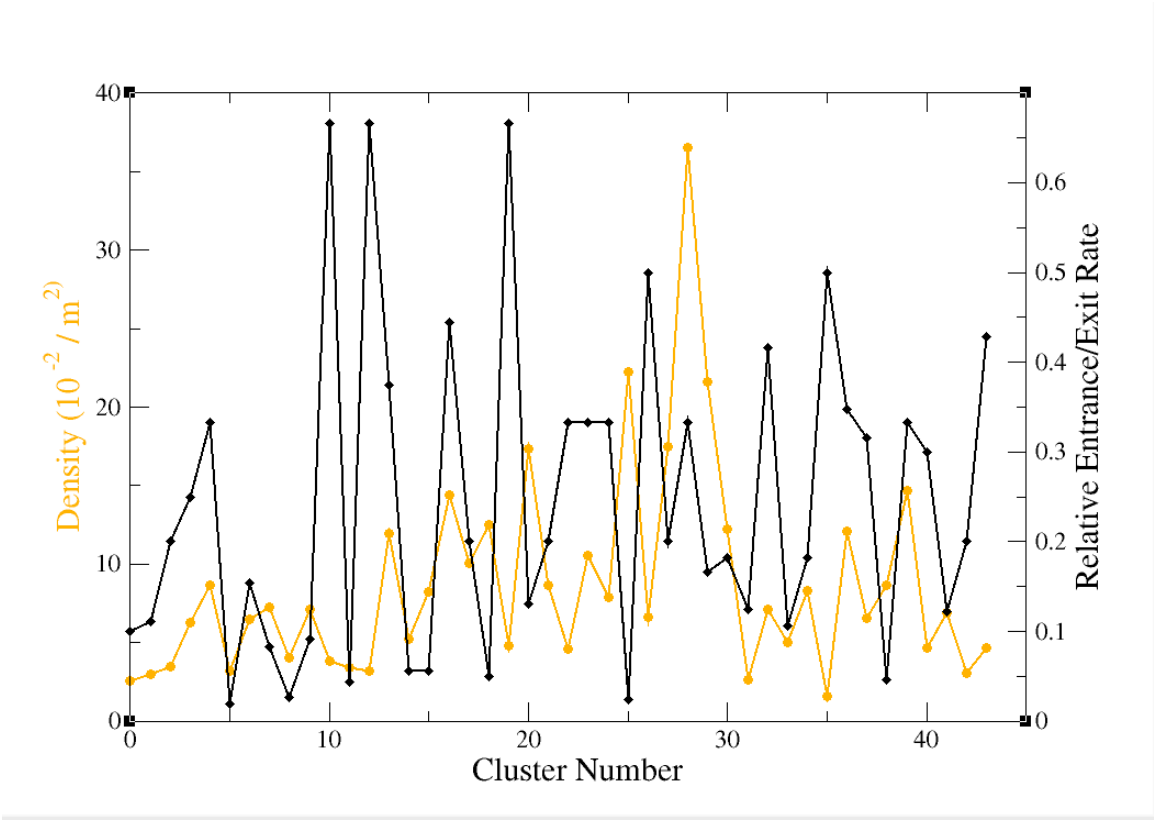


Figure 4.19. The density ($10^{-2}/m^2$) of points within a cluster in relation to the amount of times the fox exits and returns to that cluster (flux rate) for fox, F3, collared in the summer of 2014.

Figure 4.20. An example of all GPS fixes collected by female fox (F3) over a period of 16 days during August 2014. The areas labelled C1-C10 represent the emergence of clusters over time indicating areas of high use.

4.5 Discussion

This study demonstrated some interesting results that were not anticipated. Given the boundary effects and confinement due to the urban matrix, it was expected that food resources would be restricted to certain, well defined, locations, and, as such, the movement patterns were expected to be more directed towards such locations. For this reason a theoretical correlated random walk model (CRW) was tested as our "null hypothesis" for overall movement behaviour. However, all the movement paths that were collected from GPS collared individual foxes demonstrated a more random-style foraging pattern. In particular, the plots of net-squared displacement versus step number invariably fell below theoretical predictions based on a CRW (Figure 4.1). This corresponds to sub-diffusive movement, characterized by such random-style foraging patterns. It is important to note, however, that confinement effects and the distribution of urban structures (i.e. roads, buildings, fences) that are associated with urban landscapes may alter the movement patterns of resident wildlife.

Although the overall patterns were similar for individual foxes, there were some differences in the mean squared displacement. For example, M2, a juvenile male fox collared in the winter exhibited a notably higher mean squared displacement, even at shorter lag times. This is not surprising however, as snow cover and winter temperatures likely contribute to a more scarce distribution of resources, within Charlottetown, making longer movement bouts over shorter periods of time necessary to obtain adequate

amounts of food. What we did find surprising, nonetheless, was the fact that the mean squared displacement exhibited by M2, despite snow cover, remained sub-diffusive. Fox F2 also demonstrated sub-diffusive movement during the winter. Again, when resources are scarce one would expect the movement pattern to be better described by a Lévy-like walks which are characterized by super-diffusive movement patterns.

Previous studies conducted on rural foxes on PEI by Johnson (2005) and Jenkins (2010), observed movement indicative of Lévy walks (LW) during the winter months. The characteristic super-diffusive movement of LWs promotes efficient foraging when resources are sparsely distributed based on more new sites being visited over a shorter period of time (Berkolaiko et al. 1996, Larralde et al. 1992, Viswanathan et al. 2008, Jenkins 2010). LWs are known for maximizing foraging efficiency considering prey encounters for predators that are larger and faster than their targets (Viswanathan et al. 2002) such as foxes. This search strategy has also been observed in similar sized canids such as the side-striped jackel (*Canis adustus*) (Atkinson et al. 2002). Although food is more difficult to find in the winter, LW search strategies may not be required in urban areas due to the availability of resources, both natural and anthropogenic. Although Charlottetown is the largest city on PEI, it is small compared to other metropolitan centers around the globe and may be more similar to a semi-urban town. It is possible, therefore, that Charlottetown's relatively low human density, as well as geographic organization offers urban foxes sufficient amounts of natural resources found in city parks, urban golf courses, large residential backyards and pockets of vacant and protected

land throughout the urban matrix to be successful. However, it is also important to note that residents of Charlottetown are notorious for deliberately feeding the foxes via food scraps being left outside as well as hand-feeding. A recent survey conducted in Charlottetown reported that 32% of respondents (n = 286) have participated in feeding foxes in the past or would be willing to feed the foxes in the future (Martin 2015). This suggests that handouts provided by Charlottetown residents may also be a valuable resource for urban foxes within PEI and thus, the distribution of such resources may influence corresponding movement patterns.

When examining individual movement characteristics such as the mean squared displacement it is important to keep in mind behavioural traits that may differ between gender as well as the habitat types and corresponding ranges found within the individual ranges. For instance it is likely that the larger mean squared displacement of fox M2 may be a product of having a larger home range than the other foxes (See Chapter 3). A larger range is likely to include a greater variety of habitat types and therefore resource selection within an urban area. While it doesn't appear that LW search strategies need to be employed for foraging efficiency, longer movement bouts over shorter time scales may be helpful in efficiently scouting for potential mates during the winter breeding season.

The adult female fox that was collared in the winter time, F2, has a lower mean displacement than M2, even though data was collected at very similar times. This may reflect potential differences in denning behaviors. During the months of February and

March, breeding females spend much of their time searching for, and preparing den sites (Harris and Baker 2001). While the male collared in the winter may be focused on longer movements to find a mate, the female may demonstrate more localized movement within her home range, specifically around the den site she has selected (such as F2).

In the fall of 2014, a juvenile female (F4), was collared and had very similar movement patterns to F2 who was collared in winter. This could be due to a very similar home range occupied by both individuals. It is quite possible that F4 is the offspring of F2 based on the age of both foxes as well as their corresponding home ranges (see Chapter 3). Another interesting observation from the mean squared displacement demonstrated by these two foxes (F2 and F4) is the decrease that occurs around step 10 followed by an increase around steps 15-20 (Figure 4.1). This type of movement may be reflective of a spiral-type searching pattern, where the individual tends to make several turns in a row in the same direction (left or right) and is a very efficient mode of searching in areas of high resource availability (Bell 1991, Turchin 1998). This type of search mechanism, where individuals move in gradually larger loops from their starting point, is used to exhaustively search an area and have been known to be efficient in clumped or patchy landscapes (Turchin 1991, Zollner and Lima 1999, Conradt et al. 2003, Barton et al. 2009). Animals that have successfully used such search modes include the Mexican bean beetle (*Epilachna varivestis*) (Blau, Turchin 1998) and select species of birds searching for a home (Bell 1991). The fact that both individual foxes occupy the same range and utilize very similar search strategies supports hypotheses within the

literature, that movement is influenced by resource abundance and distribution in a particular area for a wide variety of mammals (Isbell et al. 1998, Wilmshurst et al. 1999, Prange and Gehrt 2004). In fact, these effects have been known to be greater in solitary carnivores, in particular females (Sandell 1989, Prange and Gehrt 2004). This is related to the reproductive success of solitary females and how the ability to effectively exploit and obtain resources is associated with overall fitness (Prange and Gehrt 2004). These patterns may also indicate that search strategies utilized in the winter do not deviate from search strategies employed in the fall for that particular area and that similar resources are available all year round.

Foxes M1, F1, and F3 demonstrated the lowest mean squared displacement during the time of data collection. All of these foxes were juveniles and were collared between August and November. The smaller distances on average, travelled by these foxes could reflect two things: 1) their age 2) the landscape composition of their home range. Juvenile foxes begin to disperse from their natal range between six and nine months old (Lloyd 1980, Harris and Baker 2001). It is possible that these young foxes had not yet begun the dispersal process and movement was still restricted to areas in close proximity to their natal den site. These foxes also live in areas of the highest-human density with less open green space. With many residents feeding the foxes in Charlottetown, we assume that in areas of higher human density there may be more people participating in this activity. With more people providing food, it is likely that these foxes do not need to make more

extended foraging efforts characterized large mean-squared displacements in order to obtain sufficient resources.

In addition to net-squared displacements, move length distributions can be used in movement analyses to gain insight into foraging strategies that would require such selections. The foxes in this study that demonstrated exponential move length distributions (F1, M1, F4) were all collared in the fall. An exponential distribution of move lengths is representative of Brownian or random movement (Gautestad 1993, Jager et al. 2013). This result is consistent with what we observe with the net-squared displacement analysis in that movement is sub-diffusive in nature with short distances being covered by the foxes even at longer lags. This type of movement indicates that resources are plentiful and long movement bouts are not necessary to reach resource abundant food patches. Resources within Charlottetown are likely to be abundant during this time as snow cover is not an issue and rodents and birds are easily accessible. This type of move length distribution is observed in multiple animals existing in resource-rich habitat such as the silky shark (*Carcharhinus falciformis*) tracked through productive waters in the North Pacific (Humphries et al. 2010), and wandering albatrosses (*Diomedea exulans*) when utilizing shallow ocean shelf habitats (Humphries et al. 2012).

In contrast to exponential move length distributions, move lengths that follow heavy-tailed power-law distribution are characteristic of Lévy walks in which long move lengths are employed to reach distant foraging patches (Ramos-Fernandez et al. 2004, Humphries and Sims 2014). Although none of the foxes in this study exhibited move

lengths following a power-law distribution, the foxes collared in the winter (F2 and M2) as well as our fox collared in late summer, also did not demonstrate exponential move length distributions. In fact the distribution that best fit the move lengths of these foxes was logarithmic. Selecting move lengths that do not represent neither Lévy nor Brownian patterns may indicate more complex movement representative of a combination of both foraging strategies (Benhamou 2007, Humphries et al. 2012). This result is not surprising for our winter foxes (M2 and F2), and may indicate that snow cover may require the foxes to use move lengths which are more in-consistent in length than in exponential distributions in order to obtain resources that may be more scarce during the winter months. These move lengths, however, are not long enough or frequent enough to constitute a power-law distribution and therefore this type of movement may indicate: 1) foxes are likely able to find sufficient resources despite the challenges of snow cover within the urban environment based on the abundance of natural and anthropogenic resources or 2) that Lévy-like movement patterns do exist, however, the confinement effects and obstacles associated with the urban landscape may be limiting the frequency of long, linear movement bouts between habitat patches thus construing patterns that may emerge for the same fox in non-urban areas (Estevez and Christman 2006). The move length distributions of fox F3, who was collared in the late summer of 2014, similar to those foxes collared in the winter, also indicate movement that is a combination of random walks. This was unexpected as we assumed that with the likelihood of natural resources being most abundant this time of year, that movement would demonstrate more

random-like characteristics. It is possible that the combination of random walks that is present is based on the frequent use of specific areas of her home range and the distances that happen to exist between them. For example, clusters of GPS points emerge in several areas, but are particularly obvious in two distinct regions of her home ranges separated by approximately 400 m (Figure 4.20). The relatively few GPS points detected between these two areas suggests that movement may be more linear when travelling between these two areas and consequently explain the logarithmic move length distributions that are expressed with this individual.

One of the characteristics of a CRW is that the turning angles are distributed in a Gaussian fashion around **0**°. When paths for all of the foxes were assessed on individual days, it was determined that the majority of the paths consisted of turning angles that were uniformly distributed around **360**°. This would tend to correspond to a more random movement pattern. The few days in which the movement demonstrates directional persistence, and turning angles remain concentrated around 0°, could indicate more directed travel for reasons related to dispersal behaviour or foraging expeditions. Additionally, in many cases of urban wildlife, semi-natural corridors such as powerline passageways, stream or creek banks and the edges of residential backyards may be used for movement within fragmented city environments in order to avoid detection by humans or predators resulting in movement paths characterized by directional persistence. For example, a study conducted on the dispersal of Roesel's bush cricket (*Metrioptera roeseli*) demonstrated more directed movement when the animal used

corridors compared to the movement of crickets navigating through the matrix (Berggren et al. 2002).

The random distribution of turning angles, demonstrated by foxes in this study could also be resultant of small home range sizes. Recent studies indicate that the home range sizes of many carnivores that reside in urban environments are smaller in size than those of rural carnivores of the same species, due to a higher concentration of food resources and the absence of predation and hunting practices (Sálek et al. 2014, Iossa et al. 2010, Bateman and Fleming 2012). These smaller range sizes could lead to the foxes turning in the opposite direction every time they reach their home range boundary leading to a more uniform distribution of turning angles. Such confinement effects on turning angle distributions were also demonstrated in a population of grey seals (*Halichoerus grypus*) in and around Sable Island (Austin et al. 2004). In the seal study, turning angles of resident seals that were restricted by the boundaries of the island, were uniformly distributed whereas turning angles of seals that were participating in foraging expeditions, off the island, were more non-uniformly distributed, implying more direct movement was being used to locate food patches.

Although range boundaries may play a role in the distribution of turning angles, another important determinant may be the distribution patterns of food resources within the landscape (McIntyre and Weins 1999). For instance, a study conducted on rural foxes during the winter on PEI (Jenkins 2010), recorded turning angles that were clustered around 0°. While this distribution may be partially indicative of larger home ranges sizes

characteristic of rural foxes, it also may be resultant of scarce resources typical of a winter landscape. Movement paths in such unpredictable and resource-poor environments may reflect search strategies required more widely distributed resources (Viswanathan 1999, Fauchald et al. 2000, Roshier et al. 2008) and thus more linear patterns may evolve.

It must be noted, that linear movement paths may not always consist of turning angles that are clustered around 0 °. Uniformly distributed turning angles may persist despite linear movement when the animal is alternating left (L) and right (R) turns that are small in size, resulting in directional persistence. By examining both the turning angle distributions and the net-squared displacement together, however, it is possible to gain further insight into the specific behaviours of animals. For example a fox that exhibits a net-squared displacement higher than the theoretical predications for a CRW is demonstrating super-diffusive behaviour. That is, the fox is covering a lot of distance in a short amount of time. Thus, if this foxes' turning angle distribution is uniform, it is likely that the fox is still moving linearly, although alternating small L and R turns throughout the movement. Conversely if a fox is exhibiting sub-diffusive behaviours when considering the net-squared displacement and demonstrates uniformity in the turning angle distribution it is likely that due to the lack of distance being covered at higher and higher lags, that animal is likely moving in a random patterns that may be representative of foraging within a resource rich patch.

While movement metrics such as the net-squared displacement and turning angle distributions may provide us overall path information, it is also important to obtain move-

based information to understand the underlying mechanisms that give rise to the emergent path behaviour. Movement based analysis, such as serial autocorrelation analysis, can provide insight into scale-dependent movement patterns. This in turn may help us determine how the animal is responding to its environment at different spatial scales as well as what landscape features at these different spatial scales may be affecting the movement behaviour.

When examining the autocorrelation turning angle data for pooled paths, it appears that turning angles do not demonstrate strong autocorrelations (Figure 4.2) suggesting that directional persistence is not present and movement is representative of a more random pattern. Pooling the data of movement paths, in order to obtain an average of turning angles and move lengths at each lag for each individual fox, is beneficial in that it increases the statistical robustness of the analysis as well as provides additional insight into environmental interactions. In saying that, performing autocorrelation analysis on pooled data can also be problematic with respect to habitat heterogeneity. For this study, however, foxes conducted individual movement paths in a relatively homogenous way, in that they utilized similar areas of their respective ranges on a daily basis throughout the duration of data collection to such a degree that areas of GPS fix clusters emerged over time (e.g: Figure 4.20). For this reason we believe that the artificial detection of autocorrelation was not demonstrated through pooled data analysis.

Further caution, when using pooled data, must be demonstrated as pooling data may limit the accuracy of the calculations to that of the lags associated with the shortest

path. For this reason, autocorrelation in turning angles and move lengths was also examined at the individual level to ensure accuracy as correlation estimates have a high variance and thus long path lengths are required to detect non-zero correlations (Nams 2013). In autocorrelation analysis a value of 1 indicates turns are very autocorrelated (i.e., all in the same direction) whereas a value of -1 indicates turns that are in the opposite direction when separated by a certain lag. Although individual foxes expressed similar patterns each day, slight differences did exist between the movement patterns of individual animals (Figures 4.3-4.5). This suggests that internal (e.g., behavioural) as well as the external (e.g., environmental) factors could be responsible for variations in temporal autocorrelation. As a result of environment, a fox residing in a highly urbanized area (i.e., downtown core) could result in turning angles that are not autocorrelated due to the abundance of anthropogenic structures existing there that may prevent straight movement paths, as well as the lack of open space that may be indicative with linear movement. Furthermore, smaller home ranges, due to boundary effects, tend to destroy autocorrelation in turning angles. For example, the home range size of fox F3 is much smaller than that of fox M2 (88 ha and 1406 ha respectively) and corresponding autocorrelation of turning angles is lower for F3 at a lag of 1 than it is for M2 at a lag of 1. At a lag of 1, both foxes have travelled for 15 mins. The lower autocorrelation values that exist for F3, could correspond to the fox reaching her home range boundary if she travels for 15 minutes, causing her to select a new turn angle. With M2, autocorrelations do not drop to < 0.6 until approximately lag 2 (30 minutes). This could indicate a larger

range and more space for the animal to move linearly hence demonstrating similar subsequent turning angles. With regards to internal factors, the degree of autocorrelation expressed by an individual during movement could also be indicative of the life stages the animal is experiencing during the time of tracking. Dispersing juveniles, for instance, will often travel in linear paths in order to efficiently seek out an area where they can establish their own territory. This may result in a lack of autocorrelation in turning angles as small L and R turns are alternated to head in a particular direction whereas opposite trends in turning angles may be observed when an adult female fox is denning. During this time several turns in one direction may be observed as the female searches for optimal den site locations, forages within a patch or remains near the den site to supervise and protect young resulting in highly correlated turning angles. Such movement restrictions resulting in high autocorrelation have been previously reported in female grizzly bears during cub-rearing (Dahle and Swenson 2003).

The autocorrelation analysis for the move lengths of individual foxes demonstrated a greater degree of variation than the turning angles. The subsequent increases and decreases in autocorrelation that are observed for individual paths are likely due to changes in movement modes (i.e., searching, travelling, resting etc.) associated with the patchiness of the environment. Negative autocorrelations are also present in many of the individual movement paths. The switch from positive to negative autocorrelation may be related to the transition of movement modes based on spatial scale (Nams 2005). For example, at smaller spatial scales (e.g., a lag of 1), a fox foraging

within a patch may exhibit move lengths shorter than the average move length as resources within this patch are plentiful and only short move lengths are necessary to acquire such resources. When the resources from this particular patch have been exhausted, the fox leaves the patch, and at a larger spatial scale (e.g., lag of 3), begins to search for the next foraging patch and is now demonstrating move lengths that are longer than the average move length and thus the animal will more efficiently reach new foraging patches (Turchin 1998). When the animal encounters another foraging patch, move lengths are likely to shorten once more. When the animal switches from move lengths that are shorter than average to move lengths that are longer than average, or vice-versa, negative autocorrelation is observed. Although some degree of autocorrelation is present in the movement paths of foxes in this study (specifically at lower lags), due diligence was taken in the form of path filtration processes and thus we ascertain that these correlations are not a product of the sampling approach, but exist due to the biological behaviour mechanisms of red foxes as well as the direct environment that they are exposed to.

Negative autocorrelations in the turning angles of a foraging animal indicate that the animal is turning one way and then the opposite way sequentially for a period of time (Turchin 1998). This type of random movement may represent the searching behaviour of generalist species within a habitat patch (McIntyre and Wiens 1999, Bender and Fahrig 2005). A form of cluster analysis was therefore employed to examine potential patterns of patch use in areas where movement data demonstrated clustering. Cluster analyses have

many applications in plant and animal ecology and have been historically used to describe and compare spatial and temporal communities or individual species in heterogeneous environments. With the development of GPS technologies, cluster analyses allows for insight into finer scale movement and patterns of resource use. A study conducted by Moorter et al. (2010), for instance was able to use cluster analysis to distinguish different movement states of free-ranging elk and in combination with recorded head movements was able to identify inter-patch foraging movements, intra-patch foraging movements and states of rest. Another study conducted on wolves in Scandinavia investigated wolf kill rates in the field based on GPS clustered data that was updated on an hourly basis (Sand et al. 2005). Similar to our work on urban foxes, both of these studies used GPS data to identify clustering and examine habitat patch use.

In this study, for all foxes except for F1, cluster sizes < 50 m^2 were most prevalent. This is not surprising due to the nature of urban environments and the heavy fragmentation that exists there. The high frequency of small patch sizes used by urban red foxes may also indicate their ability to detect resource patches at a fine spatial scale, based on two key assessment requirements: the ability to determine patch boundaries (Benrec 2002, Nolting 2013) as well as the ability to assess the resource abundance within the patch (Schmidt and Brown 1996, Beniot-Bird et al. 2013). Consequently, these assessment capabilities increase the opportunity for the forager to efficiently manage the time spent in these patches in accordance with the variation of resources that exist there (Iwasa et al 1981, Valone and Brown 1989, Schmidt and Brown 1996). As previously

mentioned, a recent survey reported that 32 % of Charlottetown respondents (n=286), are feeding or have fed foxes in the past (Martin 2015). The patches that foxes are selecting at smaller spatial scales, in many cases, may correspond to the backyards of residents providing food resources to the foxes. As well, foxes are generally more active at night with a tendency to increase activity at dawn and dusk (Ables 1969). Hence, it is also possible that the patches that are being selected are not always used for foraging, but for daytime resting sites in which the animal remains in an area of cover (i.e.: backyard shrubs, wooded areas of city parks). Within the urban matrix it is conceivable that smaller areas of cover (i.e., habitat patches of < 50 m^2) are more abundant than larger natural patches for such rest sites.

All of the cluster distributions in this study follow a discrete positive logarithmic distribution with one parameter and long right tail. For the foxes in this study, this translates to a high frequency of small cluster sizes and a lower frequency of large cluster sizes. This type of logarithmic distribution is also observed in other ecological systems such as relative species abundance (Fisher et al. 1943, Williams 1964, Kempton and Taylor 1974) in which most species are rare and relatively few species are abundant within an area. Other natural processes that exhibit logarithmic distributions include chemical reactions, autocatalytic processes and diffusion as a function of time (Koch 1969, Grönholm and Annila 2007). In all cases for this study, the less frequent larger clusters of each fox correspond with large natural areas within each of the individual foxes' home range. For example, the largest cluster demonstrated for fox M1 exists as a

large treed lot in a residential neighborhood, for F3, the largest cluster is located in a natural area that includes a stream, wooded areas and long grass. For both of these foxes, den sites were also found in these natural areas. It is likely that both of these juvenile foxes, therefore, still use these areas as a home base, that is, an area where they feel safe and confident in obtaining resources.

Trends associated with the time spent within each cluster indicate that there is also a logarithmic relationship between the frequency of clusters and the number of minutes spent within these clusters (figures 4.18-4.20), meaning that there is a statistically higher probability of a fox in Charlottetown will spend a short amount of time in a cluster or patch than a long period of time. For all foxes, with the exception of F2 the typical residency time was between 15-45 minutes. It must be noted that a residency time distribution for F1 was not created due to GPS fix issues. Similar to the cluster sizes, residency time is likely associated with foraging efficiency or resting. If the animal is foraging, this time period may be more specifically related to the "giving-up time" (GUT), which represents the time spent in a resource patch before the forager ceases searching and transitions to a travelling state in search of the next resource patch (McNair 1982, Eliassen et al. 2007). The residency time is dependent upon the occurrence of prey within the patch and also the quality of the habitat within the patch (King 2011). The residency time that is most common for F2 is 45-60 minutes with additional spikes between 120-135 minutes and 210-225 minutes. The longer time spent within patches for this adult female could be due to denning activity such as den preparation and possibly

tending to young based upon the time of year (February-March) and the breeding status of the individual. These results may also be representative of a longer fix time of this particular GPS collar (every 30 minutes rather than every 15 minutes). It is possible that observing this fox at a coarser temporal scale resulted in, what appeared to be, longer residency times.

In addition to spending time in one particular area for the purposes of foraging, the residency time could also indicate how long foxes are resting. Resting sites are key areas for many mammalian species as they provide shelter, protection from predators, and thermoregulatory stability and can affect reproduction, survival, population density and the ability of that species to exist in urban areas (Brown et al. 2014, Carvalho et al. 2014, Carvalho 2015). Although we found evidence for very few studies that quantify resting duration of medium carnivores such as foxes, two separate studies report the mean rest periods of both arctic foxes in an oil development area (Eberhardt et al. 1992) as well as red foxes in suburban areas of Toronto (Adkins and Stott 1998) to be less than two hours. This time interval encompasses the majority of the residency times observed for the foxes in this study, with the exception of F2; however, as previously mentioned, it is likely that this female is exhibiting denning behaviours where denning females have been known to spend longer rest periods at den sites during the day (Servin et al. 1991, Travaini et al. 1993). It is possible that multiple clusters per day may be indicative of urban rest sites, as multiple diurnal rest sites have been reported in Melbourne, Australia where foxes, on average, utilized 2-5 rest sites per day (Marks and Bloomfield 2006), and foxes in the city

of Bristol, UK utilized as many as 11 rest sites per day (Baker et al. 2004, Baker et al. 2001).

Further analysis on the cluster data was conducted to gain insight into the underlying mechanisms driving particular patch use behaviour. For instance, by examining both the density of GPS points within a cluster along with the relative entrance/exit rate, we are able to investigate if that animal is remaining in a small area or a large area for substantial periods of time, or if the cluster exists because the animal returns to this area multiple times per day, indicating strong site fidelity. An area of low density, along with a low relative entrance/exit rate may indicate areas around a den site for example. Generally these types of clusters are located in large natural areas and provide ample cover for young foxes, low human disturbance, and areas that would provide a variety of resources food such as berries, rodents and insects. Foxes may be able to remain in this area for long periods of time and obtain all necessary resources. Smaller natural areas within the urban matrix may also be used for similar purposes but may have higher densities of GPS points along with a low relative entrance/exit rates. These types of habitats support fox kits for the first 3-4 months of their lives (Harris and Baker 2001) and are relatable to our research, as most of the foxes captured in this study were juveniles. Remaining in the area of their natal den, despite denning season being over, suggests that we are observing these foxes pre-dispersal and they may not yet be ready to leave their natal territory. With the exception of fox F3, our data supports this explanation as, clusters characterized by a low density of GPS points as well as a low

entrance/exit rate correspond to areas where known dens are located. Based on the age of the foxes as well as their observed home ranges, it is likely that the foxes were born at these den sites. In the case of fox F2, who is an adult female, the low density of points and low entrance/exit rates may indicate den preparation behaviour rather than pre-dispersal behaviour.(Figures 4.21- 4.23). Several of the foxes also demonstrated similar behaviour in areas where no den site had been previously located. In such cases, as demonstrated by fox M2 and fox F3 for example, these areas are large residential backyards. It is likely the foxes utilize the vegetative cover in these yards when humans are not present. Similar behaviour has been reported frequently in the city of London, UK, where the most important diurnal shelter sites for foxes were quiet gardens and backyards of residential homes (Harris 1981, Marks and Bloomfield 2006). Likewise, smaller natural areas within the urban matrix may also be used for similar purposes but may be indicated by higher densities of GPS points along with a low relative entrance/exit rates. Fox M2 offers an example of this type of cluster behaviour on February 8th 2014, in a patch of vegetation separating two residential backyards. This scenario is less common for the foxes in our study, however, suggesting that larger natural areas are preferred for extended resting or denning sites.

In contrast, a cluster with a lower density of GPS points, but a high relative entrance/exit rate could indicate an area of profitable foraging. For example, particular vacant properties within the city may be composed of long grasses and bordered by a small woodlot may be an ideal area for foxes to forage for rodents such as mice, voles

and shrews. Being a relatively large space, the GPS density of such a site may remain low. Foxes may return to this habitat patch several times per day to exploit the resources found here. This pattern has been observed in foxes F2 and F3 whose home ranges are comprised mainly of an urban golf course. For these foxes, clusters characteristic of a low density of GPS points and high relative entrance/exit rates correspond with natural areas within the home range that could potentially be areas of favorable foraging. A good example of one such cluster belongs to fox F2 and is found near the shore of the Charlottetown Harbor in close proximity to a grassy area and small stand of trees. In addition to prey items such as rodents and birds that may be found here, the opportunistic nature of the fox would allow exploitation of shoreline resources such as small fish, crustaceans and shorebirds.

This pattern could also evolve when foxes are actively being fed by humans. Foxes may return to a residential property several times per day to check for food that has been left out. In fact, this pattern has been presented by several foxes in areas where it has been reported that residents leave food out for foxes on a regular basis. For example, data for fox F4 indicates a high site fidelity for a particular property owned by the PEI government for the use of road salt storage. Personal communication with a former employee of the department of highways confirms that several people working within this property feed the foxes on a daily basis, explaining the fox's high fidelity for this industrial site.

Cluster behaviour characterized by a high density of GPS points and a high relative entrance/exit rate is the least common for the foxes in this study. A possible explanation for this pattern of behaviour may be the movements of female foxes who are rearing kits and thus constantly searching for food resources to sustain themselves as well as their young. Without venturing too far from vulnerable pups, it is likely that the movement of denning females involves frequent movement bouts to and from the den site. Similar patterns of high site fidelity within small stable areas were recorded in urban-suburban raccoon populations due to the immobility and vulnerability of nursing young (Rosatte et al. 1987, Hadidian et al. 1991, Prange et al. 2003, O'Donnell and DeNicola 2006). It is likely this behaviour pattern was rare among the foxes in this study based on the lack of data collection during kit-rearing in accordance to specific animal care protocols.

4.5.1 Conclusions

Movement behaviour is particularly complex in high functioning carnivore species, such as the red fox, which actively search for prey by exploiting the habitats most often used by that prey. The level of complexity, only increases in urban environments as, in addition to natural fragmentation, there exists physical anthropogenic barriers such as roads, buildings and fences which ultimately lead to enhanced confinement effects. Such confinement on animal movement may therefore give rise to random-like movement at small spatial scales, such as within a patch, nonetheless, urban landscape features may also be responsible for random-like movement at larger spatial scales. Hence, it is quite

possible that despite our results, foxes are indeed moving with directional persistence, in the form of a CRW, both within habitat patches as well as outside of these patches. Directional persistence is a likely feature of fox movement based upon the innate behaviour of highly cognitive animals to use some degree of memory to return to habitat rich patches.

Although we believe this to be the case, we cannot say for certain as, for this study, we did not have the means to detect habitat patches within Charlottetown at the micro-habitat spatial scale necessary for such analysis. Despite these results, which elude to random-like movement, memory effects and site fidelity are demonstrated through the analyses of areas of elevated point densities (clusters) as foxes seem to utilize certain profitable areas of their home ranges with greater intensity than others and return to these areas on a daily basis. Thus, it is possible that random-like movement, with some degree of directional persistence, could exist as a result of confinement and physical barriers have modulating effects on fox movement within the urban matrix.

Some differences in movement features did emerge with respect to the seasons in which the foxes were collared. While move length distributions of foxes collared in the fall demonstrated movement indicative of a random nature, winter foxes demonstrated movement that appeared to be more complex, likely, on account of the distribution of resources and the obstacles that are associated with snow cover. Despite differences in the move length distribution, other components of the movement analysis (i.e., net-squared displacement, correlation analysis) suggest random-like behaviour persists

through all seasons. Thus it is possible, that additional anthropogenic effects, such as the food that is provided by humans, act to normalize (buffer) movement behaviour of urban species such as the fox. That is, in natural habitats, where the effects of snow cover generally result in a scarcity of resources, may be diminished in urban areas where many residents are providing food resources to the foxes on a daily basis.

Although we did not possess the means to measure specific habitat patches within Charlottetown, rigorous GPS observation allowed us to detect patch-like behaviour in all foxes through cluster analysis, with a higher frequency of smaller patches being utilized for short periods of time. Smaller habitat patches are characteristic of urban environments and thus shorter time periods are likely required for exhausting the resources here. That being said, the use of such patches in this study demonstrated variation based behavioral and environmental factors associated with individual foxes such as gender roles and the land use contained within respective home ranges. While differences in move length distributions of foxes collared in different seasons indicate an adjustment in movement patterns in relation to the season, the distribution of patch sizes, along with the time spent in such patches remains the same further indicating that foxes are using patches of similar size year round, although the distance between such patches may change based on snow cover and associated obstacles.

Site fidelity to certain habitat patches within Charlottetown may be determined by den site locations (particularly for juvenile foxes), consistent sources of both natural and human-provided food, as well as, suitable diurnal resting sites. Our results suggest

that although foxes in this study elect to spend their time in more natural areas, they will actively exploit resources provided by humans, with tendencies to not remain in these areas for long periods of time but to check back on them frequently.

Studies dedicated to obtaining information regarding the movement patterns of urban wildlife should remain to be a priority for researchers and wildlife management officials, alike, as they provide important information surrounding the ecological behaviour of wildlife within the confines of highly fragmented urban areas as well how these behaviours may differ from rural landscapes. This study indicated, that the movement of Charlottetown's foxes was related to some form of human activity. The ability to educate urban residents on the potential hazards of living in such close proximity to wildlife remains pertinent to the well-being of humans, domestic pets and the foxes themselves. Some recommendations for future studies on urban foxes in PEI would be as follows: 1) To obtain movement data over a longer period of time. Although we have learned the importance on collecting data at a fine temporal scale in order to obtain key behavioral information, it would also be beneficial to observe how individual foxes may alter their movement patterns based on seasonal changes as well as important life events such as dispersal, mating and kit-rearing. 2) To develop a means to quantify habitat fragmentation within Charlottetown and complete a multiple-scale analysis of habitat patch existence within the urban landscape in order to further investigate movement patterns at multiple spatial scales.

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Chapter 5

General Conclusions

The primary goal of this study was to examine the urban ecology of red foxes in Charlottetown with respect to key behavioural mechanisms such as selecting den sites, home range size and preferred habitat use and movement patterns resultant of foraging strategies. Understanding how urban dwelling species, such as red foxes, are affected by anthropogenic influences is becoming increasingly important as the majority of the human population resides in such urban environments. The continued urbanization of natural lands, necessary for the growing human population, is likely to lead to the decline and local extinction of many species worldwide. Thus, in order to preserve urban wildlife, it is important to investigate the traits and mechanisms that may determine the success of species living in urban environments.

Problems that have been known to arise with the co-habitation of humans and animals in urban areas include: nuisance issues such as property damage inflicted from animals denning and foraging for food as well as noise and odors that are typical of wild animals, along with, public health issues such as zoonotic disease transmission and propagation and more frequent attacks on humans or domestic pets. In order to prevent such issues it is imperative to understand the habitat preferences and the mechanisms that drive habitat selection processes within urban areas. By identifying where potential conflicts may occur, it may be possible for wildlife officials to manage and protect specific areas of high wildlife use and thus limit negative interactions with humans.

Red foxes have become one of the most globally successful urban canids due to their highly plastic diet and habitat requirements as well as their large geographic range. In Prince Edward Island (PEI), Canada, it is likely that foxes began colonizing urban areas to avoid competition and conflict with larger carnivore species in the province and have since continued to be very successful in urban areas across the province. Similar to foxes existing in rural environments, foxes in urban areas are known to establish and defend home ranges in order to maintain adequate resources for the purposes of maximum reproductive success. Within such home ranges, foxes also demonstrate habitat selection processes which define areas or habitats that are preferred by the animal which are generally used disproportionately to availability. Habitat selection can be based on the predation or mortality risk of an area, localized food availability and key reproductive behaviours such as denning and kit-rearing.

Movement between areas of preferred habitat becomes increasingly difficult in urban areas as levels of habitat fragmentation are intensified due to vast amounts of infrastructure such as roads and buildings. Thus by examining areas foxes prefer to occupy, what resources are present to influence such use and how they move between these areas were able to gain an overall understanding of how foxes are utilizing urban landscapes in PEI.

Not surprisingly, we found that foxes in Charlottetown selected for areas of low human disturbance, for not only den site locations, but also for general habitat use. Despite the time of year, or the gender of the fox, areas such as natural green spaces and extents of low human use (i.e., golf courses, vacant lots) remained profitable within individual home ranges and were used with a greater intensity than other areas despite their disproportionate availability. This is likely due to such areas offering increased natural food resources such as rodents, birds, insects, wild fruits as well as more vegetative cover for shelter and diurnal resting sites.

Although the foxes in this study elected to spend most of their time in areas characterized by low levels of human disturbance, their opportunistic nature and cognitive ability induce the frequent exploitation of easily obtainable anthropogenic resources as well. Cluster analysis results, as well as extensive anecdotal evidence, indicate that in many circumstances site fidelity is demonstrated for locations in areas of high-human use. This is likely due to humans providing the foxes with resources which require no energy expenditure on a daily or weekly basis.

The study of animal movement patterns can give us insight into how animals perceive and interact with their environment. In terms of foraging strategies, we expected to observe directionally persistent movement to resource rich patches within the assumedly patchy landscape of the urban environment. The movement patterns for all foxes analyzed in this study, however, demonstrated a more random-like foraging strategy that is characteristic of an animal foraging exclusively within a resource-rich

area. Hence, it is possible that in combination with the natural food resources available in Charlottetown, as well as the supplementary food resources provided by residents, that foxes have an abundance of food resources available to them and therefore require foraging strategies designed for concentrated resource detection. Alternatively, it is possible that such movement indicators are not conducive to urban areas as confinement effects and physical barriers disrupt natural foraging patterns and thus continued research in this field is required.

Although sample sizes in this study were relatively small, subtle seasonal differences in habitat use and movement patterns were observed. These differences are primarily attributed to the challenges of snow cover for foraging practices of carnivores such as red foxes, as well as, reproductive behaviours that occur in different seasons such as: juvenile dispersal, mate selection and kit-rearing.

In conclusion, this study provides important baseline information on key ecological indicators with regards to urban red fox ecology on PEI. By protecting and expanding areas within the urban matrix that offer an abundance of natural food resources and vegetative cover, as well as establishing educational programs for Charlottetown's residents, it may be possible to direct fox use to areas of low human disturbance and consequently limit the potential for negative fox-human interactions.